ENERGY AND NUTRIENT DIGESTIBILITY AND UTILIZATION IN GESTATING SOWS FED FIBER-RICH CO-PRODUCTS

SIGRID JOST WISBECH

PhD THESIS · TECHNICAL SCIENCES · 2023

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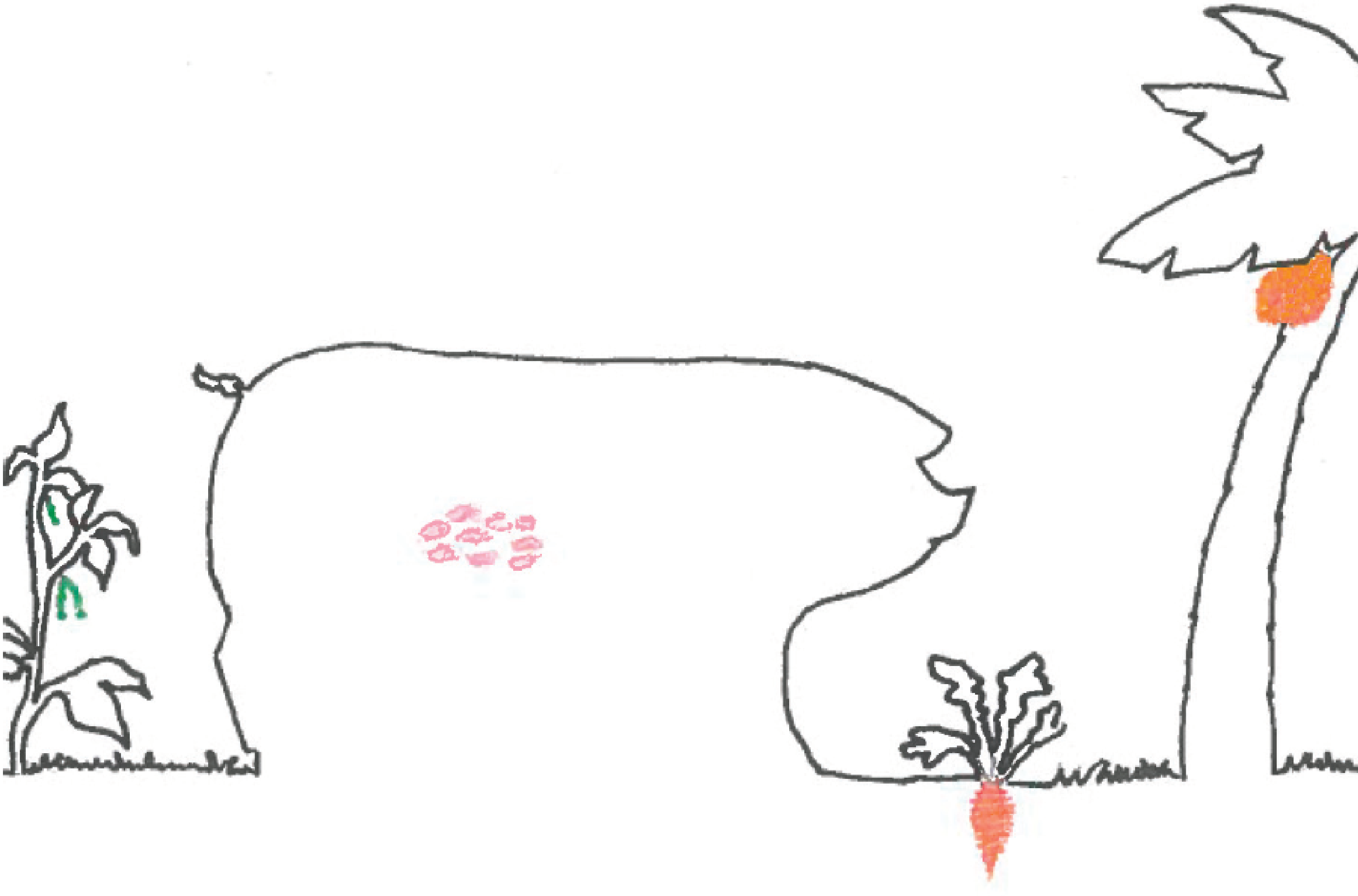

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In memory of Peter

PREFACE

This thesis is based on research conducted during my enrollment as a PhD student from February 2019 to February 2023. The “Fiber ensures an effective retention of backfat in sows” (Fibre sikrer effektiv aflejring af soens rygspæk) project, short; FibSo, funded by the Danish Pig Levy Foundation (SAF), is the main overall project, from which the results presented in this thesis derive from. Also data from the project “Processing of co-products from the vegetable food industry to improve health and welfare of growing pigs and sows” (Forædling af biprodukter fra vegetabilsk industri til forbedring af slagtesvins og søers sundhed og velfærd), short; CoFibSo, funded by the Danish Ministry of Food, Agriculture and Fisheries and KMC, Brande, Denmark; Danisco Sugar A/S, Assens, Denmark; CPKelco ApS, Lille Skensved, Denmark; Agro Korn A/S, Videbæk, Denmark; Prodana Seeds A/S, Odense, Denmark and DLF Trifolium A/S, Roskilde, Denmark was included.

Besides being funded by the Danish Pig Levy Foundation through the FibSo project (2/3) the PhD project was funded by the Graduate School of Technical Sciences (GSTS) at Aarhus University (1/3).

The overall thesis work aims to investigate the energy and nutrient value of diets containing fiber-rich co-products, when fed to dry sows.

The thesis is divided into sections, starting with an introduction and literature review of the research field together with aims and hypothesis. This is followed by a description of the experiments and account of the methods used and the three included, papers. The last section contains a general discussion followed by conclusions and perspectives.

Sigrid Wisbech

AU, Foulum, October 17th 2023

ACKNOWLEDGEMENTS

This PhD has been quite a journey. With ups and downs both privately, as well as professionally.
Thanks to all of you who believed in me, often more than I did myself – Thanks!

I would like to say thanks to many colleagues in Foulum. During my PhD I have been part of three different coffee rooms besides at times mainly being in the stable. First G22, then D20 and finally F20 – thanks for the informal talks both the professionally relevant ones, those lifting the mood and everything in between. Also thanks to both lab technicians and not the least the stable personnel– thank you very much for doing a great job helping me!

I am grateful for all the talks with my fellow PhD students: I could not have done this without you, I am sure I will have a lasting friendship with after this.

Thanks to my family and friends, thank you for supporting me – also at the very darkest parts of this journey. And of course my children; Emilie and Simon - for just being you, hugging, smiling, talking sweethearts, I Love You!

Then there is the "The Theil group", especially Maria Eskildsen, Trine Pedersen and Signe Nielsen – you have been my saviors so many times, thanks a lot! And also Liang, Jakob and Takele, thanks for helping and supporting me when needed.

Last, but not least, I would like to thank my supervisors – Thomas Bruun, you have been here from beginning to the end, being a big support and taking your time to help me when needed. Tina Skau Nielsen, who came "on the team" when I was struggling (almost) the most, being a very big support and keeping the focus on the structure and step-wise goals.
Thanks also to Knud Erik Bach Knudsen for stepping in as my main supervisor and Henry Jørgensen as hidden supervisor, when Peter got sick and later passed away.

Now to the truly difficult part – because I miss you and you should have been here with me – this PhD was just the beginning of the work you wanted to do. Increasing the knowledge of the shifts in energy pathways when sows reestablish fat-depots. Thank you, Peter K. Theil for giving me this opportunity - I learnt so much from you.

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SAMMENDRAG (DANISH SUMMARY)

Interessen for at inkludere fiberrige restprodukter, såsom sukkerroe pulp, soja- og ærte-skaller i foderet til søer er stigende. I den cirkulærer bioøkonomi kan visse restprodukter, som ikke er egnet som human føde, blive et højværdiprodukt hvis det omsættes af husdyr. Restprodukterne er meget forskellige og viden om produkternes energiværdi til søer er begrænset, men dette er vigtigt både i forhold til velfærden for dyret og påvirkningen af miljøet ved udskillelse af næringsstoffer.

Først og fremmest er det vigtigt at bestemme fordøjeligheden, men også udnyttelsen af både energi og næringsstoffer af forskellige restprodukter iblandet foder til søer, hvilket er emnet for denne afhandling. I forsøget på at belyse dette, er der gennemført to eksperimenter, og resultaterne er sammenfattet i tre videnskabelige artikler, hvoraf to er publiceret og en er ved at blive trukket tilbage og erstattet, det opdaterede manuskriptet er inkluderet.

I eksperiment 1 indgik 48 drægtige søer, der blev tildelt stigende mængde sukkerroe pulp i foderet (119 til 217 g total fibre/kg) i tidlig og midt drægtighed. Søerne var endvidere delt i tre grupper afhængig af deres rygspæk-tykkelse (artikel I). I den efterfølgende drægtighed fik søerne iblandet en af fire fiberkilder; sukkerroe, sojaskaller, palmekage eller et fibermix (176 til 243 g total fibre/kg) (artikel II).

I eksperiment 2 indgik 8 tomme, ikke-lakterende søer, der fik en af otte diæter: en basal diæt eller basal diæten kombineret med en af syv fiber kilder; frøskaller, mask, kartoffel pulp, ærteskaller, pektin affald eller sukkerroe pulp (402 til 495 g total fibre/kg tørstof) i et ukomplet overkrydsnings forsøgsdesign (artikel III).

Sukkerroe pulp, fiber mix, ærte- samt sojaskaller blev fundet egnet til delvist at erstatte høj værdi afgrøder som korn i foderet til ikke lakterende søer, fordi både fordøjeligheden af energi (83 til 86%) og næringsstoffer var høj, samtidig med at energien blev godt udnyttet. Palmekage, mask samt kartoffelpulp kompromitterede kvælstofudnyttelsen. Frøskaller samt pektinaffald havde en lav ernæringsmæssig værdi fordi fordøjeligheden af både energi (hhv. 44 og 67%) og næringsstoffer var lav. Desværre var det i både artikel II og III ikke muligt at kvantificere effekten af at fodre med forskellige fiberkilder i forhold til hvor effektive søerne var til at reetablere deres huld fordi dyrene var fodret tæt på vedligeholds niveau. I artikel I var der en øget protein aflejring og numerisk større fedt aflejring ved stigende inklusion af sukkerroe pulp.

SUMMARY

Fiber-rich co-products, such as sugar beet pulp, soy- and pea hulls are of increasing interest as feed ingredients in sow feed. From a circular feed economy point of view, some co-products not directly suitable for human consumption can re-enter the feed chain as human food through animals. These co-products are a diverse group of fiber-rich ingredients, and the knowledge of the energy value is limited, but important when feed is optimized, due to both health of the animal and environmental effect of output of nutrients.

First and foremost, determination of the digestibility and thereafter the utilization of energy and nutrients from different fiber-rich co-products in diets fed to dry sows, is what this project is about. To investigate this, two experiments were carried out, from which three papers has been written; two is published and one is being retracted and replaced, the updated manuscript is included.

In experiment 1, 48 gestating sows received increasing levels of sugar beet pulp (119 to 217 g total fiber/kg) in early and mid-gestation. Further, the sows were also divided into three feeding strategies depending on backfat level at weaning (paper I). In the following gestation, sows received one of four fiber-rich diets containing either sugar beet pulp, soy hulls, palm kernel expellers or a mixed fiber (176 to 243 g total fiber/kg) (paper II).

In experiment 2, 8 empty, non-lactating sows received one of eight diets: a basal diet or the basal combined with one of seven co-products: seed residue, brewers spent grain, pea hull, potato pulp, pectin residue and sugar beet pulp (402 to 495 g total fiber/kg Dry matter) in an incomplete cross-over study (paper III).

The sugar beet pulp, pea hull, soy hull and mixed fiber diets were found to be well suited to partly replace high value grain crops in dry sows, due to both a high digestibility of energy (83 to 86%) and nutrients together with the energy being well utilized. Palm kernel expellers, brewers spent grain and potato pulp were found to compromise the nitrogen utilization, while seed and pectin residue, due to a low digestibility of energy (44 and 67%, respectively) and nutrients, had a low nutritional value. Unfortunately, due to sows being fed close to maintenance in both paper II and III, no effect of fiber source was found on restoring the backfat depots. In paper I, an increase in protein retention and a numeric increase in fat retention with increasing fiber inclusion was found.

MY OWN CONTRIBUTION TO THE WORK

The “Fiber ensures an effective retention of backfat in sows” (FibSo) project was my main project and I both did the experimental plans and practically carried out the two experiments, where I collected data from. I did the statistics as well and wrote paper I and II on the results from these experiments.

The chemical analysis were carried out by lab technicians at Aarhus University, Foulum except for some of the feed analysis, which were done by Eurofins Steins Laboratory.

Data from the project “refinement of co-products from the vegetable industry to improve the health and welfare of growing pigs and sows” (CoFibSo in this thesis), was used for preparing paper III. The animal experiment and data collection were finished several years before the onset of my PhD enrollment. In collaboration with Senior Researcher, Emeritus, Henry Johs. Høgh Jørgensen the complete dataset for this paper was prepared, and I did the statistics and wrote the paper.

Furthermore, I conducted a third experiment, which was part of the Born2Live project (funded by GUDP), I did the data handling, statistics and produced some preliminary results. However, due to unforeseen challenges with the feeding in the pre-farrowing period, a scientific paper about effects of different fiber levels fed before farrowing on the farrowing kinetics in sows, was not included as a part of this thesis.

SCIENTIFIC CONTRIBUTIONS

Included papers

This thesis is based on the following three publications:

I. **Wisbech, Sigrid J.**; Nielsen, Tina S.; Bach Knudsen, Knud E.; Theil, Peter K.; Bruun, Thomas S.
Effect of different feeding strategies and dietary fiber levels on energy and protein retention in gestating sows.
Updated manuscript (replacement): Journal of Animal science. October 2023.
This is a retraction to:
Wisbech, Sigrid J.; Bruun, Thomas S.; Theil, Peter K.
Increased feed supply and dietary fiber from sugar beet pulp improved energy retention in gestating sows.
Published: Journal of Animal Science. 2022. 100, 1-13. Doi: 10.1093/jas/skac054

II. **Wisbech, Sigrid J.**; Bruun, Thomas S.; Bach Knudsen, Knud E.; Nielsen, Tina S.; Theil, Peter K.
Influence of four fiber-rich supplements on digestibility of energy and nutrients and utilization of energy and nitrogen in early and mid-gestating sows.
Published: Journal of Animal Science. 2023. 101, 1-13. Doi: 10.1093/jas/skad007

III. **Wisbech, Sigrid J.**; Nielsen, Tina S.; Jørgensen, Henry; Bach Knudsen, Knud E.
Influence of fiber-rich co-products on nutrient and energy digestibility and utilization in sows.
Published: Journal of Animal Science. 2023. 101, 1-10. Doi: 10.1093/jas/skad086

Other scientific contributions

Abstracts:

I. **Wisbech, Sigrid J.**; Knudsen, Knud E. B.; Bruun, Thomas S.; Tybirk, P.; Nielsen, Tina S.; Theil, Peter K.
Attempt to restore backfat efficiently in gestating sows using four different fibre supplements. Digestive Physiology in Pigs 2022, Amsterdam, Netherlands – *Poster*

Co-authorships:

I. Nielsen, Signe E.; Feyera, Takele; **Skovmose, Sigrid J. W.**, Krogh, Uffe; Eskildsen, Maria; Theil, Peter K.
Intravenous infusion of glucose improved farrowing performance of hyper prolific crossbred sows. Journal of Animal Science. 2021. Vol 99, No. 5, 1-11. Doi: 10.1093/jas/skab061

Nielsen, Signe E.; Feyera, Takele; **Skovmose, Sigrid J. W.**, Krogh, Uffe; Eskildsen, Maria; Theil, Peter K.
Corrigendum to: Intravenous infusion of glucose improved farrowing performance of hyper prolific crossbred sows. Journal of Animal Science. 2021. Vol 99, No. 5, 1-1. Doi: 10.1093/jas/skab161

II. Feyera, Takele.; **Skovmose, Sigrid. J. W.**; Nielsen, Signe. E.; Vodolazs'ka, Dar'ya; Bruun, Thomas. S.; Theil, Peter. K.
Optimal feed level during the transition period to achieve faster farrowing and high colostrum yield in sows. Journal of Animal Science. 2021. Vol. 11, No. 2, 1-11. Doi: 10.1093/jas/skab040

ABBREVIATIONS AND CLARIFYING TERMS

Amino acid	AA
Apparent total tract digestibility	ATTD
Backfat	BF
Body weight	BW
Calculated total fiber	cTF
Carbon	C
Carbon dioxide	CO_2
Crude protein	CP
Deuterium oxide	D_2O
Digestible energy	DE
Dry matter	DM
Enzyme digestibility of organic matter	EDOM
Gross energy	GE
Heat production	HP
Metabolizable energy	ME
Net energy	NE
Nitrogen	N
Non-starch polysaccharides	NSP
Organic matter	OM
Short-chain fatty acids	SCFA
Soluble non-starch polysaccharides	S-NSP
Standardized ileal digestible	SID
Titanium dioxide	TiO_2
Total fiber	TF

Dry sows:	Non-lactating, empty or gestating, sows.
Early gestation:	Day 0-30 after estrus.
Mid gestation:	Day 30-60 after estrus.

SECTION 1. GENERAL INTRODUCTION

Globally, the need for food is as high as ever, but availability cannot keep up. The World Food Programme states it bluntly: “While needs are sky-high, resources have hit rock bottom” and describes year 2022 as: “A year of unpredicted hunger” (WFP, 2022). A way to increase the availability of food is a circular food system, where farm animals contributes to human supply while reducing environmental impact of the whole food system at the same time (Van Zanten et al., 2019). In a circular food system, the arable land is primarily used as food for humans where a big variety of co-products are produced, some are edible others non-edible for humans. The edible ones should either be avoided/limited as livestock feed or at least primarily eaten by humans, while the non-edible ones should be fed to animals. In that way, the non-edible co-products are made edible to humans in the form of animal products, Figure 1.1.1 (Van Zanten et al., 2019).

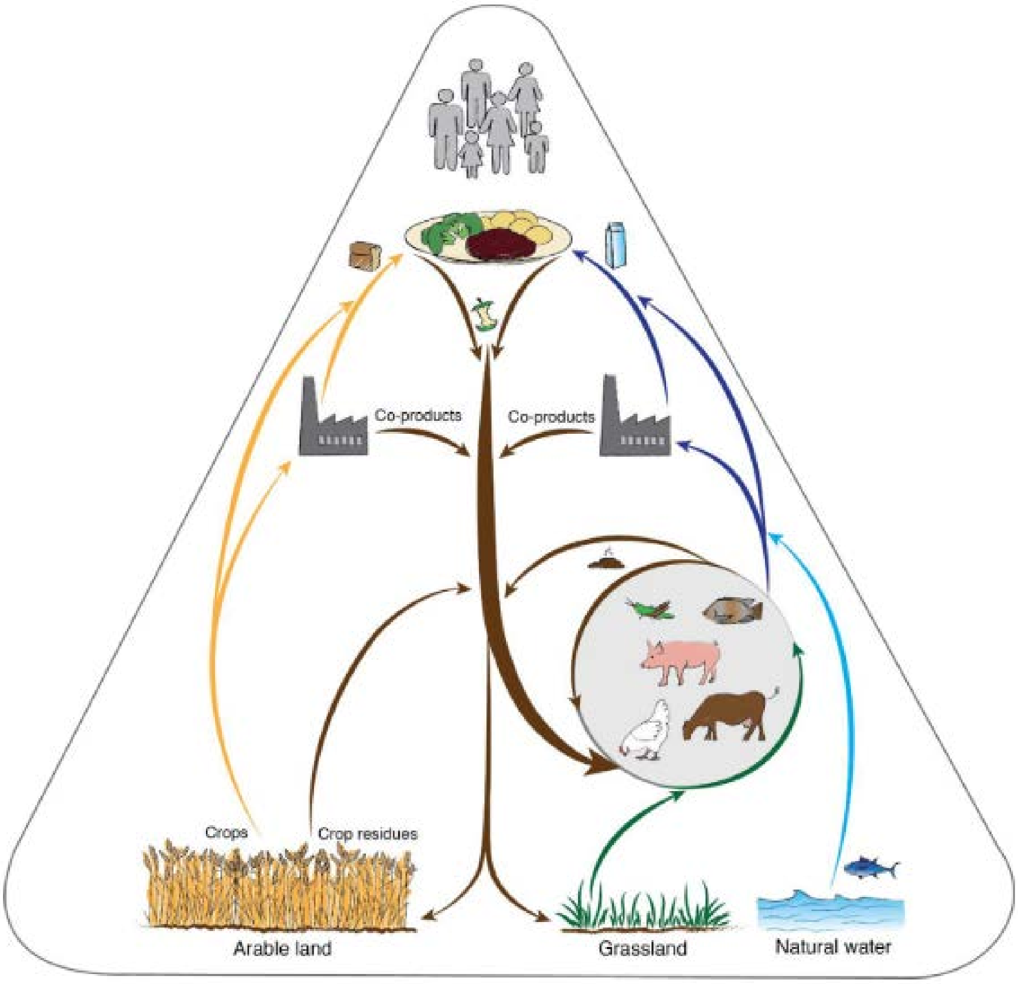

Figure 1.1.1 - The contribution of animals and recycling of nutrients in a circular food system (Van Zanten et al., 2019).

A central element here is to feed animals with feed that would otherwise have been lost for food production (Van Zanten et al., 2019). The use of co-products is a big part of this solution? (Zijlstra and Beltranena, 2022), however, they vary in nutrients, both macronutrients and protein, but especially in composition and level of dietary fibers (Zijlstra and Beltranena, 2013). As concluded by Zijlstra and Beltranena (2022), using co-products may have negative impact on animal health, growth performance, nutrient excretion among others, but these risks are possible to manage with proper feed evaluation. A main issue of co-products is the energy value, which, if underestimated, will (1) decrease the actual protein to energy ratio and (2) result in the animal being fed too much. This will unintendedly increase feed costs, excretion of nutrients, muscle growth and/or excessive fat deposition of for example gestating sows. Neither is favorable to the animal nor the farmer.

SECTION 2. LITERATURE REVIEW

2.1. Fiber-rich co-products as feed ingredients for sows

A co-product is the leftover, in some cases even regarded as a waste product, from the production of high value products or items from the food and agricultural industries, ex. sugar beet pulp from the sugar industry, pea hull from processed peas and palm kernel expellers from the palm oil industry and many others. Co-products are a very diverse group of residues that differ depending on the main material used for the production and depending on where it is produced. Furthermore, some co-products will also be available only at a certain time of year unless dried or otherwise conserved. In Europe, the most important available co-products are from the grain, root and tuber processing industries (Serena and Knudsen, 2007), while products from the bean and oil industry typically are of non-European origin, except for sunflower expellers, where Ukraine is the major producer (Ates and Bukowski, 2022).

In most cases, the co-products are high in fiber content, but also vary within each by-product, compared to grains ex. barley, see examples in Table 2.1.1 (Serena and Knudsen, 2007), often due to being the “cover” part of the plant material or simply “not being” sugar, starch, protein or fat, that usually is the main product of the production.

Table 2.1.1 - Fiber composition of four co-products and barley (g×kg^{-1} dry matter).

	Sugar beet pulp[1,2]	Seed residue[2]	Pea hull[2]	Barley[2]
S-NSP[3]	407, 290	21	121	52
I-NCP[4]	177, 207	212	148	92
Cellulose	195, 203	197	452	39
Lignin	35, 37	124	9	35

[1] (Bach Knudsen, 1997)
[2] (Serena and Knudsen, 2007)
[3] S-NSP: Soluble non-starch polysaccharides
[4] I-NCP: Insoluble non-cellulosic polysaccharides

The production or purification industries are increasing worldwide, e.g., the production of raw sugar (Figure 2.1.1.) has increased from 90 mio. ton to 175 mio. ton from 1980/81 to 2016/17 leading to a side-stream of 20 mio. ton of dry mass of sugar beet pulp available annually in Europe (Joanna et al., 2018).

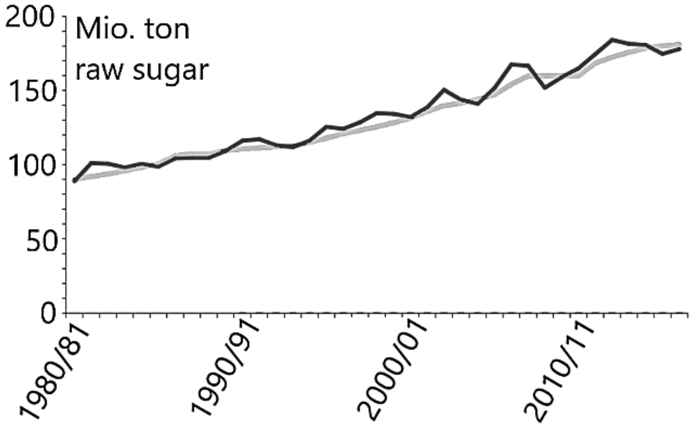

Figure 2.1.1 - Production (black) and demand (gray) of raw sugar from 1980 to 2017 globally. Translated from (Sukkerroedyrkere, 2017).

2.1.1. Definition and characteristics of fiber

Fiber is an overall description of primarily a group of carbohydrates, which cannot be degraded by enzymes in the small intestine. With the total fiber (**TF**) being defined as non-starch polysaccharides (**NSP**) and lignin (Bach Knudsen and Lærke, 2018). An important characteristic of fiber is how easily it is fermented by microbes primarily in the large intestine, which is linked to the composition of the NSP fraction and degree of lignification, Figure 2.1.2 Soluble fiber is in general easier fermented than insoluble (Noblet and Le Goff, 2001; Renteria-Flores et al., 2008), and a higher lignification decreases fermentability (Noblet and Le Goff, 2001) due to the cross linkage of NSP to lignin (Bach Knudsen et al., 2017), making the matrix structure rigid and more or less resistant to fermentation (Ruiz-Dueñas and Martínez, 2009).

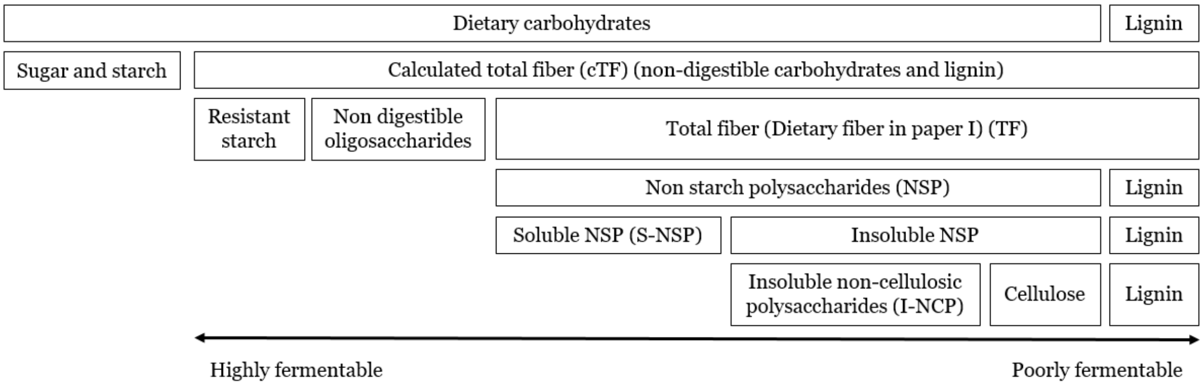

Figure 2.1.2 - Schematic presentation of the composition of fiber, modified from the review by Leeuw et al. (2008) and from Bach Knudsen (1997).

Not just the structure, but also the physiochemical properties of fibers are important. Where the important physiochemical properties are swelling, water binding and bulking properties, where co-products rich in soluble fiber or a dissociated cell wall matrix (from ex. heat treatment) has a higher swelling and water binding capacity than co-products with a high lignin content and intact cell wall matrix (Serena et al., 2007; Zhou et al., 2018b). The latter will in contrast have a higher bulking effect than soluble fiber (Mudgil and Barak, 2013; Williams et al., 2019). The high swelling capacity increases the fermentability because the matrix structure is looser, and thereby accessible for bacterial degradation, while poorly fermentable fibers will have bulking properties because they are not digested. Both types of fibers fill the gastrointestinal tract, however in different ways. The high swelling capacity and higher viscosity of soluble fibers decrease the rate of emptying the stomach and intestine, compared to insoluble fibers, where transit time is medium in the stomach and fast through both ileum and colon (Hansen, 2012). Compared to a diet low in fiber, high fiber diets had twice as high transit time in ileum and colon, but a longer transit time in the stomach (Hansen, 2012). Even though transit time is higher when sows are fed diets high in fiber, a study by Le Goff and co-workers found the retention time sufficiently long not to negatively affect the fecal digestibility of energy (Le Goff et al., 2002).

As for energy, the digestibility of nutrients is highest when the fibers are high in soluble fiber, due to the increase in swelling and decrease in retention time (Le Goff et al., 2002; Renteria-Flores et al., 2008). Fiber inclusion affects both digestibility of energy and nutrient of the fiber-rich ingredient as well as in the other ingredients. Nutrient digestibility is in general decreased with increasing total fiber levels (Ramonet et al., 2000a; Noblet and Le Goff, 2001; Holt et al., 2006), however more in non-fermentable fiber-rich diets compared to highly fermentable ones. This is due to the nutrient being linked to these fiber structures and the way the nutrients are more or less unavailable to enzymatic degradation in the small intestine and, if the fiber is non-fermentable, in the large intestine as well. The excretion of bacterial protein increasing, as well as when the bacterial mass and thus turnover increases, further decreasing protein digestibility unless accounted for (Ramonet et al., 2000a; Noblet and Le Goff, 2001). Renteria-Flores et al. (2008) found the nitrogen (**N**) digestibility in a high soluble fiber diet being the same as the control diet, while 3 percent point lower in a diet high in insoluble and soluble + insoluble fibers compared to the control diet. Furthermore, they found that increasing levels of soluble fiber increased digestibility of both energy and insoluble fibers, with energy digestibilities increasing from 83% in the diet high in insoluble fibers to 89 % in the diet high soluble fibers.

When the fiber-rich fraction is digested, the uptake of energy is primarily in the form of the end products of fermentation; short chain fatty acids (**SCFA**), where acetate, propionate and butyrate is the major ones and typical in the proportion 65:20:15, but depending on fiber source and quantity of substrate (Bindelle et al., 2008). The total SCFA produced is higher when the feed is high in soluble fibers compared to insoluble fiber, due to them being easier to ferment by the microbiota (Moturi et al., 2022) and both higher in SCFA produced compared to a low fiber diet (Serena et al., 2009).

2.1.2. The role of fiber as a source of energy

Both glucose, protein, fat and SCFA can be oxidized, Figure 2.1.3. When glucose is present, it will be oxidized, and all cells can use glucose as an energy source for oxidation. When the supply of glucose from the gut is higher than the glucose needed in tissues, glycogen can be synthesized and later used for glucose supply, but when the glycogen depot is depleted, glycogenic substrates, including propionate, can be used in the gluconeogenesis to synthesize glucose (Sjaastad et al., 2010). When glycogen stores are full, excess glycogen will be stored as triglycerides in adipose tissues.

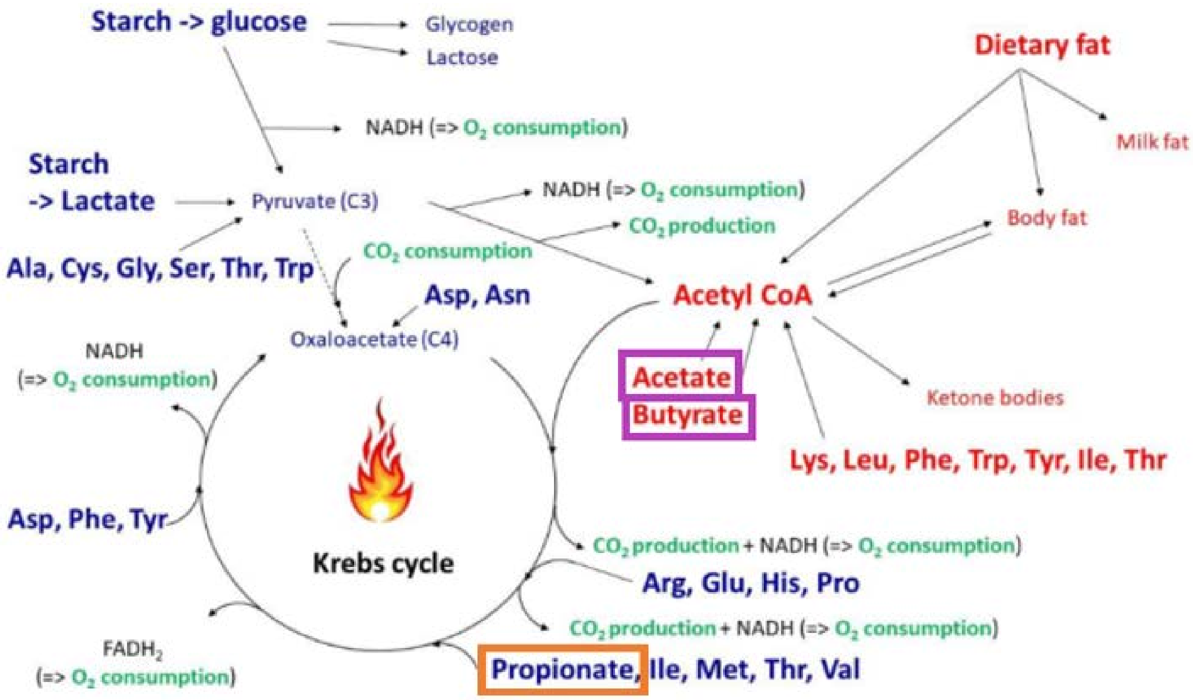

Figure 2.1.3 - Overview of the intermediary energy metabolism, with the short chain fatty acids (SCFA): Acetate, butyrate (ketogenic energy) and propionate (glycogenic energy) highlighted. (Theil et al., 2020).

The end-products of fermentation are SCFA, the main SCFA being acetate, propionate, and butyrate. The SCFA are absorbed from the gut lumen in the large intestine and transported via the portal vein to the liver, where propionate and butyrate are taken up by the liver, and potentially used for gluconeogenesis, cholesterol and fatty acid synthesis.

In contrast to acetate and butyrate, propionate is a glycogenic precursor, when it is taken up by the liver, where it can be used directly in the citric acid circle as energy, Figure 2.1.3. Acetate and butyrate can both be used for oxidation in different tissues. Furthermore, they can also be used as precursors for Acetyl-CoA (Figure 2.1.3), which can be used for de novo lipogenesis both in the liver but also in the adipose tissue (Sjaastad et al., 2010; Theil et al., 2020).

When glucose is used as a precursor for de novo lipogenesis, one carbon dioxide (**CO_2**) molecule per pyruvate molecule is lost, when pyruvate is turned into Acetyl CoA (two CO_2 molecules per mole glucose). The other way around, when using Acetyl-CoA as substrate for oxidation, 2 molecules of CO_2 is lost when entering the Krebs cycle (Theil et al., 2020).

Apart from being potential substrates for oxidation and fat retention, SCFA also have a regulating effect on the balance between de novo fat synthesis, lipolysis and fatty acid oxidation, favoring fatty acid oxidation and removal of non-esterified free fatty acids from the blood (Bach Knudsen et al., 2017). If the overall goal is to gain body fat, a combination of a high energy intake and SCFA uptake has potential to favor fat retention (Williams et al., 2017). The level of glucose in portal blood peaks around one hour after feeding, and then drop to the level from before feeding within 4-5 hours, while uptake of SCFA is rather stable all day. When feeding sows a high soluble fiber diet (440 g TF/kg dry matter [**DM**]) compared to a low fiber diet (177 g TF/kg DM), the blood glucose peak will be lower, whereas blood SCFA concentration will be rather stable throughout the day, thereby reducing the diurnal variation in energy supply. Feeding a high fiber diet compared to a low fiber diet, resulted in an approximate doubling of the absorption of SCFA, Figure 2.1.4 (Serena et al., 2009).

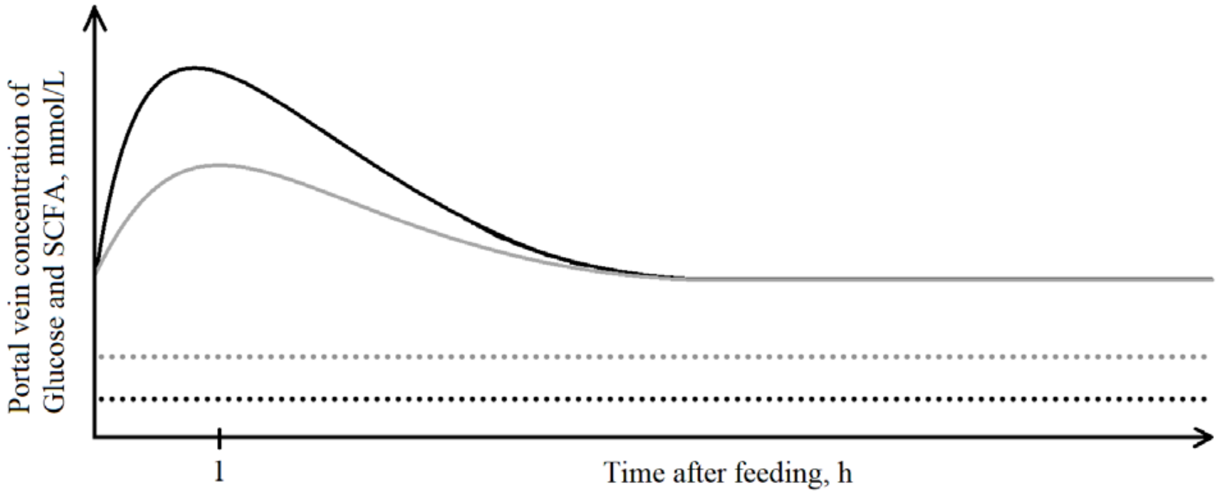

Figure 2.1.4 - Portal vein concentration of glucose (line) and short chain fatty acids (SCFA) (dots) when sows were fed either a low fiber diet (black) or high fiber diet (grey). Rough interpretation of the results found by Serena et.al (2009).

2.1.3. Additional effects of fiber

Much research has been done regarding the various health and welfare aspects of including different types of fiber-rich feed in the diet of sows, some of them are explained more into depth below.

Satiety. The feeling of satiety is a complex matter, currently not fully understood (de Leeuw et al., 2008). In the hypothalamus there is both an appetite and satiety center, these are activated by different hormones and nerves, among others insulin, from the pancreas and Peptide YY, produced by epithelial cells in small and large intestine, which activates (by negative feedback) the satiety center. While stretch sensors in the stomach releases ghrelin, which activates the appetite center. The stretch sensors are activated when the stomach is empty (they tighten the stomach) (Sjaastad et al., 2010). The effect of insulin is more pronounced in diets high in starch compared to high fiber diets (Hansen, 2012), however the insulin sensitivity can be increased with increasing SCFA levels (Tan et al., 2016).

Even though the pig has been domesticated it still shows foraging behavior, typically by rooting and nosing the ground while walking between different areas. This is an appetite behavior probably stimulated by ingestion of feed, while inhibited when satiety gives negative feedback (de Leeuw et al., 2008). This natural foraging behavior, can if the environment do not give the opportunity to express these behaviors naturally, lead to a few more simple unnatural oral (self- and substrate-directed) behavioral elements, like sham chewing and bar biting (de Leeuw et al., 2008). When these are shown repeatedly they are called stereotypic behavior, and can be associated with endorphins, activated by chronic stress (Cronin, 1985). The stereotypic behaviors are displayed in close relation with a meal, especially short after a meal. Behavior associated with rooting, physical activity and manipulation can be shown both right after ingestion of feed or several hours later, this can be in anticipation of the next meal (and thereby hunger) but it can also reflect prolonged satiety (de Leeuw et al., 2008). When housed in groups hunger can also be shown by aggression between the animals due to competition of feed (Hansen, 2012).

Compared to a low fiber diet, feeding diets high in fiber, both soluble and insoluble fiber has been shown to decrease stereotypic behavior (Robert et al., 1993). While Danielsen and Vestergaard (2001) found that gestating sows fed a diet high in soluble fiber, compared to insoluble fiber or a low fiber diet, showed less aggressive and stereotypic behavior as well as a decrease in time standing when fed the high fiber diets compared to the low fiber diet (Danielsen and Vestergaard, 2001). Rijnen et al. (2003), Jørgensen et al. (2010) and de Leeuw et al. (2005) also found a decrease in activity, however the latter did not, like Holt et al. (2006) find any change in the behavior (de Leeuw et al., 2005).

Oxidative stress. Oxidative stress defined by excess production of reactive oxygen species plays a part in the inflammation process, by among others causing an imbalance in the prooxidants and antioxidants (Lauridsen, 2019), which can damage lipids, protein and/or DNA (Bach Knudsen et al., 2018). This damage can potentially decrease the reproductive performance (Zhao and Kim, 2020; Li et al., 2022). In early gestation, oxidative stress can be linked to altered foetal development, and embryotic loss both pre- and post-implantation (Deluao et al., 2022), while in late gestation oxidative stress can impair feed intake, foetal development, and even cause abortion (Li et al., 2022). This could be due to the antioxidant capacity being insufficient to cope with increased oxygen tension, when blood flow in the placenta increases (Schoots et al., 2018). SCFA has shown to alleviate the oxidative stress on different parameters. Acetic acid can prevent DNA oxidative damage of the epithelial cells in the large intestine (Williams et al., 2017). Tan et al. (2016) showed that including konjack flour as a source of soluble fiber decreases oxidative stress compared to a control group. However, in both groups the oxidative stress increased with progress of gestation (Tan et al., 2016). Oxidative stress is correlated with the gut microbiota, where bacteria increasing the antioxidant capacity reduced oxidative stress and thereby the stillbirth rate in sows (Wang et al., 2019).

Fetal survival. Regarding the survival of embryos in gestation, adding fiber to the feed, also has a beneficial effect, which can be due to the changes of circulating hormones, where feeding fiber-rich diets promotes maturation of follicles and oocytes in the sow ovary (Tian et al., 2020). Over three reproduction circles, van der Peet-Schwering et al. (2003) showed an increase in 0.5 piglets/litter and a lower piglet weight at birth, when fed a diet high in fiber. A review done by Jarrett and Ashworth (2018) concludes that it is especially in studies where sows are fed high fiber diets before mating, the improved reproductive performances are found. This is explained by improving the very early stages of development of the oocyte and embryo (Jarrett and Ashworth, 2018), which can be done by increasing the uniformity of the follicles (and later embryos). This can be due to a prolonged increase in insulin production when feeding a diet high in sugar beet pulp (Wientjes et al., 2012) and/or increased insulin sensitivity when uptake of propionate increases (Xu et al., 2020).

2.1.4. Energy content in sow feed

The energy content or energy density of a diet is complex to estimate, as it may be expressed in several levels taking steps of digestion/utilization into account, Figure 2.1.5.

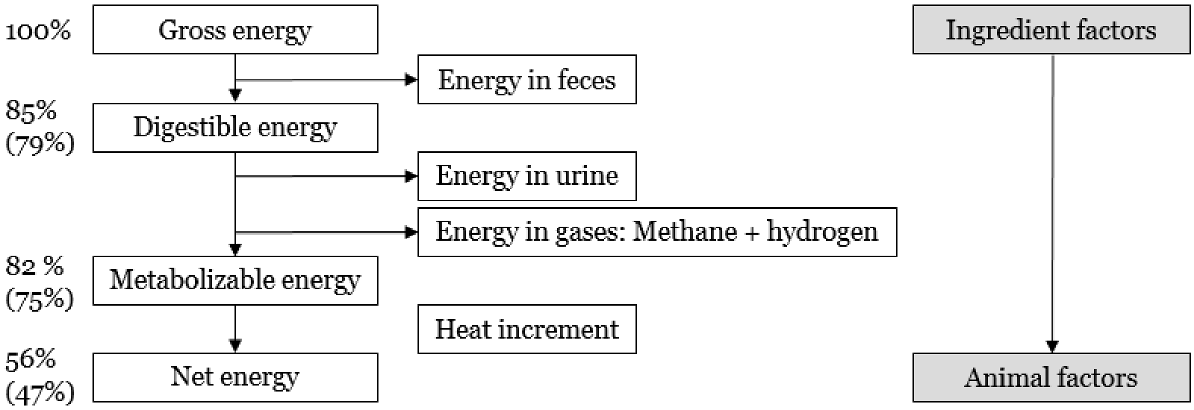

Figure 2.1.5 - Levels of energy digestion/utilization, together with the proportion of gross energy that available at the level, modified from Patience (2012) where proportions are weanling pigs fed a high digestible diet. Including proportions, in brackets, from Theil et al. (2020), in pigs fed different diets. It is further shown whether it is ingredient or animal factors that are most import in the determination.

The energy content of a feed can be determined most simply as the gross energy (**GE**) by bomb calorimetry. This is, however, an imprecise predictor for the energy digestibility and utilization in the animal. On average, 15 – 20 % of the GE in feed for pigs based on concentrated ingredients will be lost in feces, however varies (10 – 30 %) dependent on dietary composition (Patience, 2018), especially protein and fiber (Theil et al., 2020). It will vary between species and the development of the intestine, e.g., age of the animal.

The energy not lost in feces is designated digestible energy (**DE**), thus being available for utilization in the body. As DE does not take energy lost in urine and gasses (mainly methane) into consideration, the term metabolizable energy (**ME**) is used to express the energy available after correcting for the loss of energy loss in urine and gasses. Of digestible energy, around 96% is metabolizable (Theil et al., 2020).

The DE value of feeds is broadly used, because it is simple and adjusts for the fecal energy loss. Metabolizable energy is even more precise, but is often estimated from regression equations of DE, due to gases being complex to estimate and energy in urine is time consuming and somewhat imprecise to measure (Patience, 2018). Net energy (**NE**) expresses the energy available for the pig/sow for covering requirements for maintenance and productive purpose and is, if heat increment is measured/assumed correctly, an even more precise energy value. Often, NE is estimated based on calculations fitted growing pigs and maintenance-fed sows, either using DE or ME together with ingredient content of either extract (fat), starch, protein and acid detergent fiber (Noblet et al., 1994). However, these energy sources differ in efficiency dependent of the fate of energy (maintenance, fat and protein accretion), and to achieve the potential precision of the NE system, it is important to understand the proportion between these energy fates of the animal (Patience, 2012). The NE system is broadly used in Europe, and in Denmark from 1984 to 2004. Since 2004, the Danish feed evaluation system has been based on potential physiological energy, which is closely related to NE. Potential physiological energy is based on the potential quantity of ATP released by complete oxidation of digested nutrients (Boisen, 2007), estimated by in vitro analysis and assumed energy values of different nutrients (Theil et al., 2020). This system was chosen because it, in an easy and cheap way, can ensure that a specific diet is composed as expected (Tybirk et al., 2006). The unit in this system is expressed as a feed unit; a feed unit for pigs corresponds to 7.38 MJ potential physiological energy. Due to the higher fermentation capacity in sows compared with pigs, the feed unit for sows is slightly higher than for growing pigs corresponding to 7.70 MJ potential physiological energy (Tybirk et al., 2006). However, importantly, not considering the fate of energy when utilized. The potential physiological energy system assumes that all digested energy is completely oxidized, which is not 100% valid, due to some animals secrete (milk when lactating) or retain energy (Theil et al., 2020).

2.2. Use of fiber in the diet for the gestating sow

A typical European diet for gestating sows is based on wheat, barley and soybean meal, with a TF content around 15%, but it may vary according to proportions of barley and wheat, as barley increases the TF content and wheat lowers it. The Danish legislation requires that sows are fed a sufficient amount of straw, “filling” feed or feed with high fiber content, that gives a feeling of satiety and comply the need for chewing (Retsinformation, 2017).

The gestating sow is well suited for consuming and digesting nutrients from fiber-rich ingredients. The digestibility of nutrient is age dependent, especially pronounced for fermentation of fibers (Noblet and Shi, 1993; Jacyno et al., 2016), where sows are superior to younger pigs, because they have a higher fermentative capacity (Che et al.

2001; Li et al. 2019). This is due to a longer hindgut (7.5 m in a 270 kg sow while it is 4.3 m in a 30 kg pig) and thereby a longer digesta residence time (Le Goff et al., 2002). Compared to the lactating sow, the gestating sow has a lower energy requirement, and therefore needs less feed, if fed a typical gestation diet with a relatively low fiber content. The need of less feed results is restricted feeding (low DM intake) and a lower total gut fill. Gut fill is important, because it influences satiety and a low gut fill will make the sows feel hungry for a longer period of time (Jørgensen et al., 2007).

2.2.1. Influence of lactation on the upcoming gestation

The gestation period for the multiparous sow follows a lactation period, where the high prolific sow nurse up to 14-15 piglets, who will gain around 3 kg/d, mainly from drinking milk. To support this high milk production, sows typically consume close to 9 kg of feed each day, of which approximately 1.5 kg is total fiber, mainly from wheat and barley. Despite the high feed intake, the sow still mobilizes especially body fat to support milk production. In 1994 Auldist et al. (1994) found that sows nursing 14 piglets lost 8.8 mm in back fat (**BF**) and 23 kg body weight (**BW**) during a 28 day lactation period, where sows on average consumed 5 kg feed per day (Auldist et al., 1994). In 2017, Strathe et al. (2017) showed that sows consuming on average 6.1 kg per day in a 26 day lactation period lost on average 3.3 mm of BF and had a BW loss of 25.9 kg, while weaning on average 13 piglets with a total weight gain of 76 kg from d 2 till weaning.

In the last week of lactation, the subsequent reproductive cycle is initiated with the lactational anestrus where the sow starts developing the follicles. These follicles are very diverse in size and grows only a bit due to the low energy balance of the sow and the suckling of the piglets, which creates the luteinizing hormone pattern seen in Figure 2.2.1. (Soede et al., 2011). The height increases as well as the length decreases between the luteinizing hormone peaks until weaning, where the pattern shifts completely and make the follicles start to further develop (Soede et al., 2011).

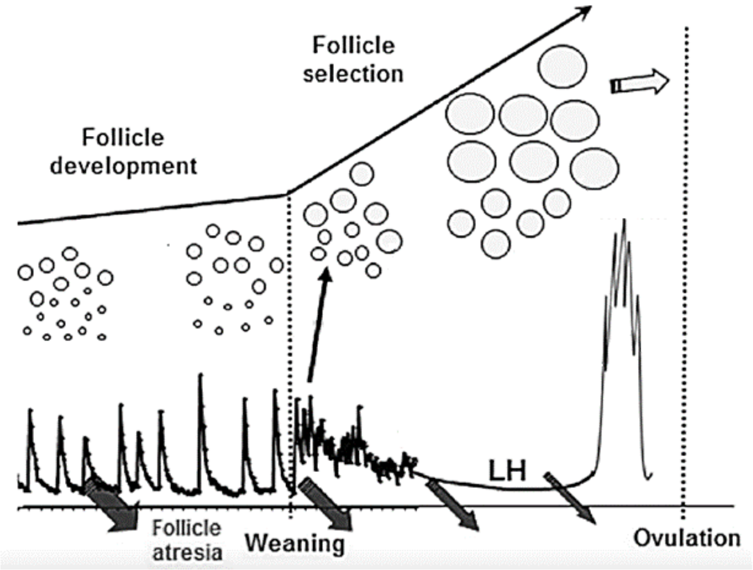

Figure 2.2.1 - Follicle development, selection and atresia before ovulation in the sow, and the pattern of luteinizing hormone (LH) (Soede, 2016).

If the concentration and pulsatility of luteinizing hormone is too low at weaning, the sow will have a prolonged weaning-to-estrus interval, which is highly dependent upon energy status of the sow (Quesnel and Prunier, 1995).

A negative energy balance during the lactational anestrus period can extend the weaning-to-estrus interval and negatively influence both number, size and viability of the follicles after weaning (Soede et al., 2011; Kemp and Soede, 2012). A study performed by Zak et al. (1997) also found that the energy balance before weaning affected the weaning-to-estrus interval, ovulation rate and embryo survival. The latter, however, only when energy intake was compromised the last week of gestation (Zak et al., 1997).

2.2.2. Partitioning between energy requirement in gestation

When sows are housed in thermal neutral conditions, energy is required for conceptus products (fetuses, placenta and mammary tissue), maintenance and maternal growth. Throughout gestation maintenance will require the most energy. While the partitioning between maternal growth and conceptus products shift as gestation progresses, Figure 2.2.2 (Gaillard et al., 2019).

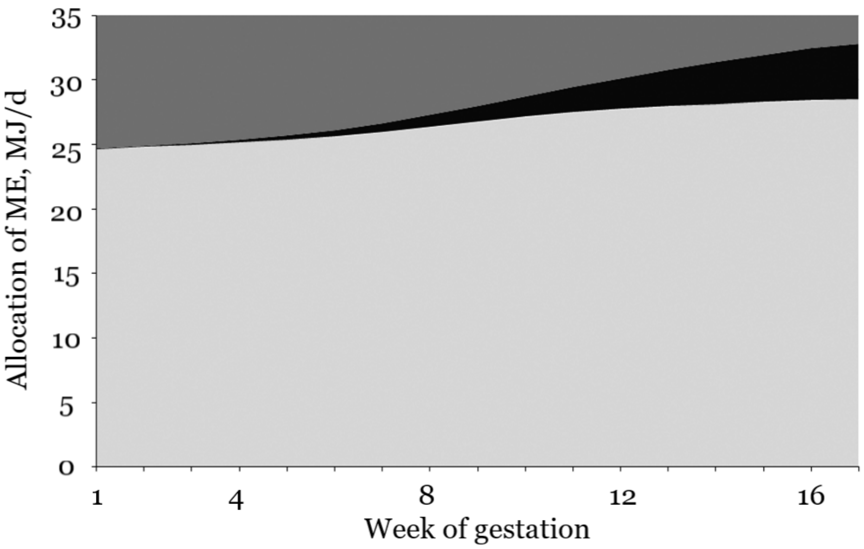

Figure 2.2.2 - Partitioning between energy requirement of maintenance (light grey), conceptus (black) and maternal growth (dark grey) of group housed sows from week 1 to 17 of gestation. Data are simulated using the InraPorc model (Gaillard et al., 2019).

Maintenance

Energy for maintenance requirement increases with the weight of the sow, and depending on the weight gain of the sow during gestation this requirement will increase as well (Gaillard et al., 2019). Maintenance is usually calculated by multiplying the metabolic bodyweight ($BW^{0.75}$ [kg]) with a constant, for ME, being 0.420 to $0.460\,{}^{MJ}/_{BW^{0.75} \times d}$, that is slightly higher than NE, 0.325 to 0.375 ${}^{MJ}/_{BW^{0.75} \times d}$ maintenance requirement, Figure 2.2.3 (Theil et al., 2020).

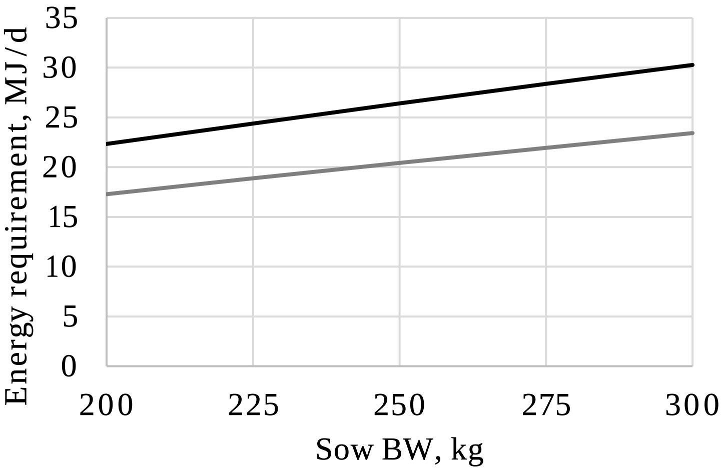

Figure 2.2.3 - Maintenance ME (black) and NE (grey) energy requirement depending on BW, using the constant 0.420 and 0.325 ${}^{MJ}/_{BW^{0.75} \times d}$ (Theil et al., 2020) calculating ME and NE requirement, respectively.

Conceptus products – well developed fetuses at farrowing

At weaning, the follicular phase is initiated and lasts for 4-7 days, then the sow is mated at estrus (time of ovulation) (Soede et al., 2011). The period until around 12-15 days after estrus (the luteal phase; the pre-implantation period), is a very sensitive period, due to both uterus (formation of the ovarian luteal tissue) and embryos (by migrating and elongating) getting ready for implantation (Langendijk, 2021). The implantation process is critical, because at this time the embryos gain contact to the mucosa of the uterus and implant for future fetal development. When more-developed embryos implant, uterine secretions increase making the environment hostile to the less developed embryos (Da Silva et al., 2016), which will have an even harder task of implantation. This favors homogeneity in embryos directly associated with homogeneity in developed follicles at estrus. Even if the less developed embryos do implant, they will still be susceptible to lack of nutrient and/or space to develop, and many will die within the next 20 days of gestation (Peltoniemi et al., 2021). If the sow is chronically stressed or lacking energy, implantation can be partly or completely compromised, resulting in either a reduced litter size or sows returning to estrus (Kemp and Soede, 2012; Langendijk, 2021). A study where sows were exposed to repeated acute stressors (grouping resulting in fighting) in either the follicle phase, early gestation or both did, however, not seem to affect farrowing performance compared to single housed sows (Soede et al., 2007). The cortisol levels of stress-exposed sows were not found to increase as it might have done if the stress had been chronic, and the authors speculated this to be the reason for the lack of effect on farrowing performance (Soede et al., 2007). Reactive oxygen species are secreted both by embryos and the surroundings. At lower levels the oxygen reactive species are necessary for normal development of the embryos, but in higher levels (Deluao et al., 2022) ex. induced by cortisol (Espinoza et al., 2017), has the possibilities to disturb, pause (Deluao et al., 2022) or even block or retard (Guérin et al., 2001) development of the embryos/fetuses.

Group-housing of sows and stocking density has the potential to cause chronic stress, and mixing of animals and fighting for food can be acute stressors (Kemp and Soede, 2012). In Denmark, as in the rest of Europe, sows are by legislation, housed in groups from weaning until a week before farrowing (Retsinformation, 2017). Often with regrouping around 4 weeks after estrus, where sows are monitored for pregnancy. During the first month of gestation, the organs in the embryo are formed, and will develop further the next month. The last two months, the fetuses gain weight and are fully developed and ready to be farrowed (Eskildsen, 2016; Peltoniemi et al., 2021).

Maternal growth - Reestablishment of body fat

The fat lost in lactation needs to be re-established in the following gestation period. A way to do this, and a widely used feeding strategy in Denmark, is to use different feeding strategies according to BF thickness at the time of weaning and preferably reassessment of the BF level at day 30 and 81 of gestation. The goal is to have uniform sows with a BF thickness of 16-19 mm (changed in 2022 to 14-17 mm) at the next farrowing (Bruun and Højgaard, 2021).

This is typically done mainly in early (d 0-30) and mid (d 30-81) gestation, by dividing the sows into three groups depending on backfat thickness (high, medium and low feeding strategy), where sows on the high feeding strategy have the greatest feeding level and those on the low has the lowest, Figure 2.2.4.

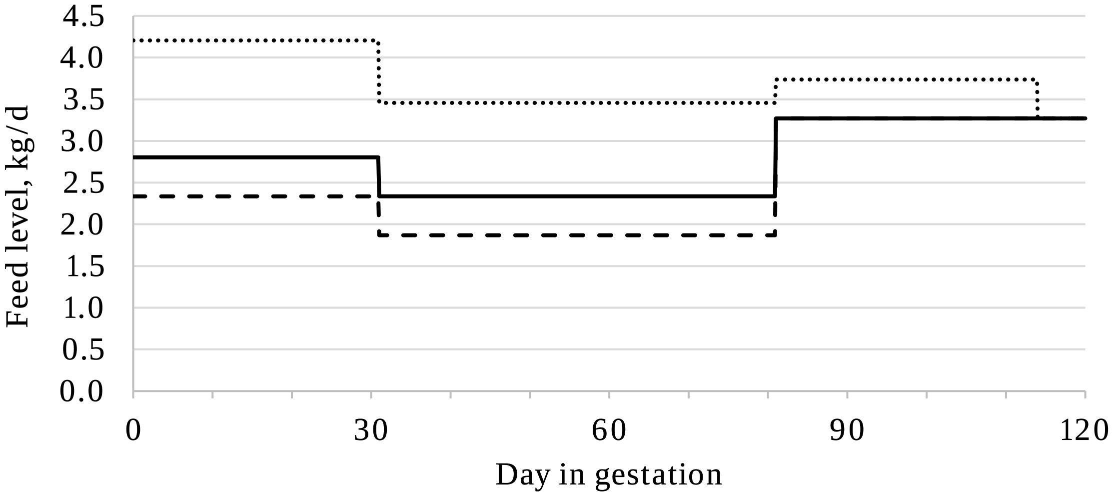

Figure 2.2.4 - Danish feed recommendations for gestating sows, the dots being the high feeding curve, solid the medium and dashed being the low (Bruun, 2019).

This feeding strategy is generic, and do not take the BW of the individual sow into consideration. The result is that backfat is re-established rapidly in low BW sows. Due to the gap between maintenance plus conceptus requirement and feeding level being greater compared to high BW sow. The low feeding levels is, ideally, as close as possible to maintenance plus with conceptus requirement and will result in a minimum of energy retention (Theil et al., 2020).

Increasing the feeding level with 30% in early gestation has previously shown to increase BW gain and the litter size with +2 piglets, whereas no change was observed for piglet birthweight with increased feeding level in early lactation (Hoving et al., 2011). The authors were not able to identify the physiological explanation for this. However, in a later published paper, the same authors found no change (also not in the opposite direction) in progesterone, luteinizing hormone or insulin-like growth receptor-1 and embryonic or placental characteristics, when increasing the feed intake with 30% the first month (Hoving et al., 2012).

Another feeding strategy is precision feeding, where energy and protein fractions is adjusted daily, depending on requirement (both maintenance and reestablishing of body fat). This makes it possible to decrease both intake and excretion of nutrients. Compared to a two phase feeding system, it is possible to decrease lysine intake and excretion with 30% and 17%, respectively (Gaillard et al., 2021). Gaillard et al. (2021) further speculates, that in an optimal feeding scenario it would be possible to feed each individual animal, depending on both day in gestation, actual daily body weight, and activity level, by combining two diets to feed the individual sows accordingly to both energy and protein requirement. Precision feeding, however, must be accompanied by multiple weighing's of the individual sows throughout gestation in order to reach the targeted gains on BW and BF.

At the moment, both energy and protein are fed according to the feeding recommendations, where each amino acid (**AA**) is expressed as g standardized ileal digestible (**SID**) AA per feed unit or kg (Tybirk, 2019). The first limiting AA is lysine (Everts and Dekker, 1994) and because of that, all other AA are fed in % of SID lysine. When feeding protein per kg feed, intake of protein will increase when feeding levels increase.

SECTION 3. AIM AND HYPOTHESES

The overall aim of this PhD thesis was to investigate the nutrient and energy value of diets containing fiber-rich co-products in dry sows.

To do this it was studied how:

- Total tract digestibility of nutrients and energy is affected by inclusion of fiber-rich co-products.
- Energy from fermentation of fiber-rich co-products in a diet is utilized when restoring fat depots.
- Inclusion of fiber-rich co-products affected physical activity and thereby potentially reducing the heat loss.

Based on the overall aim it was hypothesized that:

1. Energy from fermentation improves the utilization of energy when fed to sows restoring their fat depots. **– Paper I**
2. Apparent total tract digestibility of energy and nutrients differs between fiber source, dependent on non-starch polysaccharide composition and degree of lignification. **– Paper II and III**
3. Increasing the gut fill would decrease the activity level and thereby the heat loss. **– Paper I, II and III**.

SECTION 4. ACCOUNT OF METHODS

4.1. Brief presentation and justification of applied methodology

The following chapter is a brief presentation of experiment 1 and 2 and the applied methods together with a justification for the choice of these methods.

Only multiparous sows were included in this thesis work, primarily due to two reasons 1) they have already been in a catabolic state in their life (during lactation). 2) gilts gain considerable amount of muscle mass during their first gestation, due to a considerable maternal growth. This growth in muscle mass is not preferable in these studies

Both is important due to the focus of this is on restoring the fat depots.

4.1.1. Experiment 1 - Paper I and II (FibSo)

The first experiment (papers I and II) was carried out using 48 gestating sows (in two blocks), fed four different dietary treatments in two consecutive periods, early (d 0-30) or mid (d 30-60) gestation. The sows were housed individually, without access to straw, Figure 4.1.1.

Figure 4.1.1 - Housing of the sows.

Body weight gain was measured on a scale, and body composition estimated using both the deuterium dioxide (**D_2O**) method, GE and N balances, using fecal grab samples and six hour urine collected by catheter. Further plasma metabolites (non-esterified fatty acids, glucose, urea, lactate and triglycerides) were measured. Heat production was estimated using measurement of heart rate for four to six hours on day 15 and 45, Figure 4.1.2. Apparent total tract digestibility was estimated using the marker technique, titanium dioxide (**TiO_2**) used as the marker.

A condition for the FibSo project was that the sows were primary bought to be part of another project (Born2Live). The Born2Live project used the sows from d 108 till weaning. Therefore, the sows had to be in good condition for farrowing, and this limited our opportunities to let them gain a lot of fat during gestation.

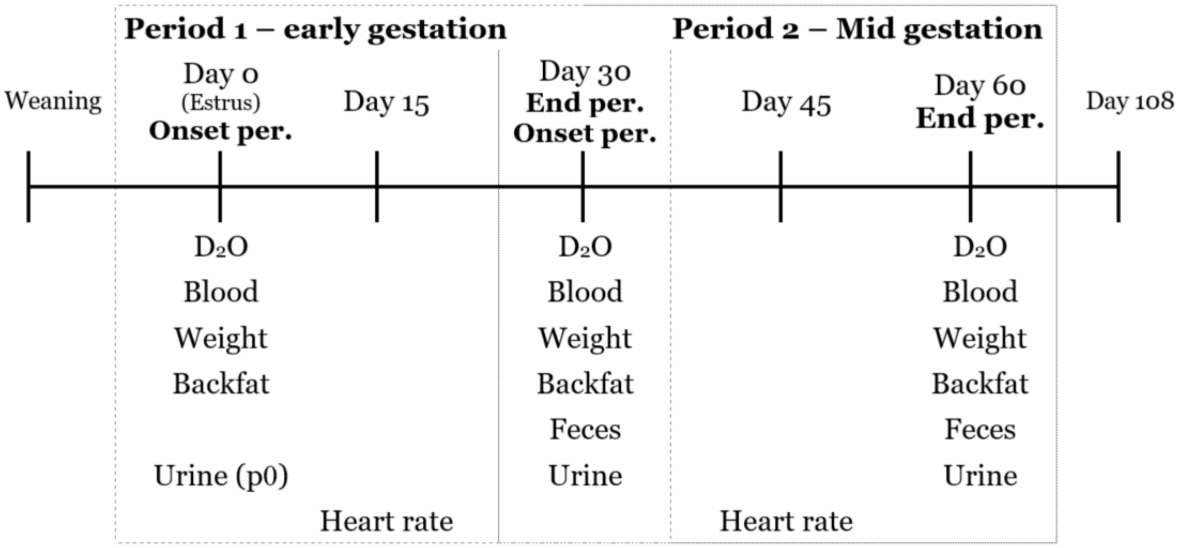

Figure 4.1.2. - Overview of the data and sample collection in experiment 1, at day 0 blood (only used for deuterium dioxide [**D_2O**], p1) and urine (for D_2O, p0).

4.1.2. Experiment 2 - Paper III (CoFibSo)

The second experiment was carried out using 8 empty non-lactating sows in a Youden square incomplete cross-over design with 7 treatments. After a transition period, of 14 days, with the new treatment, each sow had 5 days of total collection of both feces and urine in a metabolic cage. On day 2 and 3 (48 hours), the metabolic cage was moved to a respiration chamber, where both consumption of oxygen and production of CO_2, methane and hydrogen were measured together with frequency of standing, Figure 4.1.3.

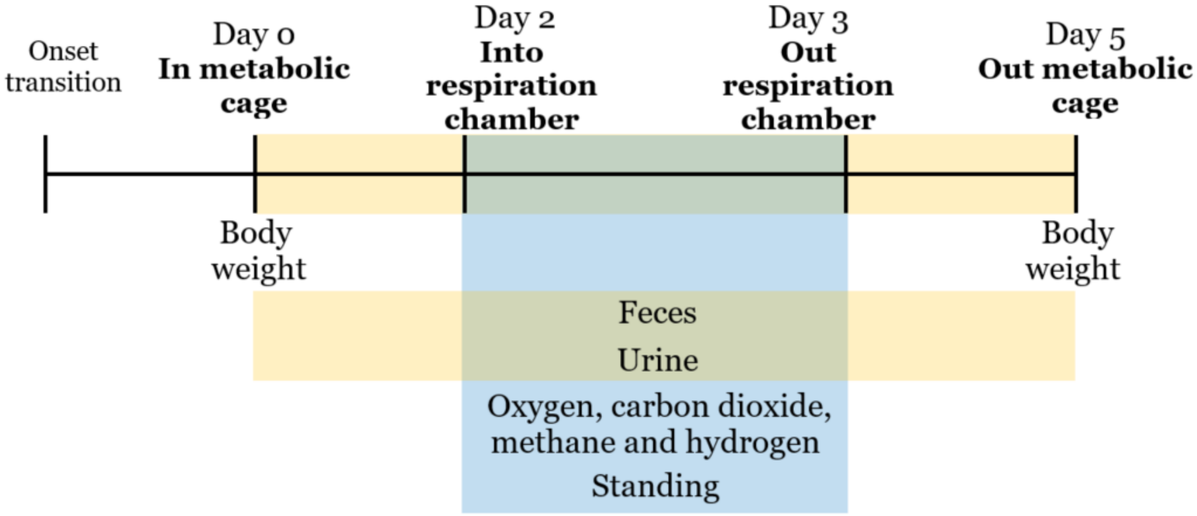

Figure 4.1.3 - Overview of data and sample collection in experiment 2.

4.2. Design

Doing an experiment close to practical production conditions (Experiment 1 in this thesis) both has advantages and disadvantages. The clear advantage is that it is easy to apply the findings at the farms, while the most important disadvantages and other possible design optimizations are:

- In experiment 1, the feed was not analyzed before onset of the experiment. Especially in paper II, it would have been a big asset to know the total fiber content, since we aimed at the treatments to provide equal amounts of total fiber. We chose to use fiber content values from the commonly used Danish database, while values of palm kernel expellers were from Bach Knudsen (1997).
- Higher feeding levels, especially in paper II, would also have been preferred. The sows should preferably have been fed to a backfat gain of at least 1%, to make the use of the deuterium method to distinguish between fibre sources more accurately. However, due to the sows being part of another project, they were not allowed to gain too much backfat during the gestation period.
- It would have been an advantage to include a basal/control diet in paper II, or at least to have used the low fiber diet from paper I as the “basal component” in paper two. This would have enabled us to use the difference method to calculate the digestibility of each fiber-rich supplement, as in paper III. Furthermore, it would also have been more accurate, if the inclusion rate of the fiber-rich supplement had been greater.
- In paper I we omitted two sows in the mid gestation period because they were the only ones on the “high” feeding strategy, when re-assessing their backfat at day 30. This re-assessment shifted many sows to the low feeding level, and thereby closer to the maintenance feeding levels, making the deuterium method less accurate. If we had chosen to keep all sows at the feeding curve from day 0, it would have increased the number of sows included, and made the deuterium method more accurate. We chose to change feeding strategy at day 30 because it is typical practice in Denmark.

In experiment 2, the sows were weighed before entering the respiration chamber and upon exit. . This was done for the same sow several times. A regression was then made, and from this the weight of the sow at the day in the respiration chamber was used. It would have been more precise, if it had been possible to weigh the sow in the respiration chamber.

4.3. Digestibility

The total tract digestibility (**ATTD**) can be determined either by total collection, typically when the sow is in a metabolic cage, or by obtaining a grab fecal sample. If using a grab fecal sample, it is necessary to add an external insoluble marker to the feed or use an indigestible feed component. The most common markers are: acid-insoluble ash (where selenite can be added to increase ash content), chromium dioxide, TiO_2 or an intrinsic marker e.g. lignin.

In experiment 1, TiO_2 was used as marker with inclusion levels between 1.79 and 2.11 g TiO_2/kg in paper I and 2.4 to 2.9 g TiO_2/kg diet in paper II. TiO_2 was chosen because chromium dioxide has carcinogenic properties, and it is cheaper to analyze TiO_2. We aimed at an inclusion rate of 3 g TiO_2/kg, mainly due to the study of Wang and Adeola (2018), who compared three levels of titanium dioxide markers (2.5, 5.0 and 7.5 g TiO_2/kg) and did not find any difference in ATTD of GE. Other studies, e.g., (Miller et al., 2016), used 2 g TiO_2/kg in the diet. The inclusion levels were lower than expected, however, assuming proper mixing of the TiO_2 and the feed before pelleting and sampling of the feed, this should not raise any concerns when using the analyzed TiO from the feed in the calculations of digestibilities.

The digestibility has been calculated, with N as an example:

$$ATTD\ N\ [\%] = 100 - \left(100\ \times \frac{Diet\ TiO_2\ [\%]}{Fecal\ TiO_2\ [\%]} \times \frac{Fecal\ N\ [\%]}{Diet\ N\ [\%]}\right)$$

In experiment 2, total collection of feces was done for 5 days, while the animals were in metabolic cages. The total amount was weighed and a subsample taken for analyses. Total collection is the golden standard. At the time the study was performed, no experiments had been carried out to determine the days necessary to collect. However, in 2020 Liu and coworkers published an article concluding that a collection period of 5 days is adequate to determine energy and nutrient ATTD (Liu et al., 2020).

In experiment 2, the ATTD, with N as an example, was calculated:

$$ATTD\ N\ [\%] = \frac{\left(Diet\ N\ [\%] \times diet\ intake\left[{}^{kg}/_{d}\right] - Fecal\ N\ [\%] \times feces\ produced\left[{}^{kg}/_{d}\right]\right)}{Diet\ N\ [\%] \times diet\ intake\left[{}^{kg}/_{d}\right]} \times 100,$$

In experiment 2, both the basal diet were fed solely and partly exchanged with one of the fiber-rich co-product, to be able to use the difference method to calculate the ATTD of the fiber-rich co-product:

$$ATTD\ N_{FRCP}\ [\%] = \frac{\left(diet_{DM}\left[{}^{g}/_{d}\right] \times diet_{N}[\%] - \left(fecal_{DM}\left[{}^{g}/_{d}\right] \times fecal_{N}[\%] - BD_{DM}\left[{}^{g}/_{d}\right] \times BD_{N}[\%]\right) \times \left(1 - \frac{ATTD_{N\_BD}}{100}\right)\right)}{diet_{DM}\left[{}^{g}/_{d}\right] \times diet_{N}[\%]} \times 100$$

where the difference between the digestibility of the total diet and basal diet (**BD**) is used to calculate the digestibility of each co-product.

To increase the precision using this method to estimate ATTD of the co-products, the basal treatment had more replicates than the diets containing the co-product.

Table 4.3.1 - Comparison between methods of used to calculate digestibility.

	Pro	**Con**
Marker (TiO_2)	Grab sample (fast, easy, anywhere)	Require analysis Proper mixing and sampling of feed Assumption of - 100% indigestible - feed source independent
Total collection	Actual total amount	Labour demanding Housing in cages Risk of leaching/ contamination Takes days

4.4. Urine

4.4.1. Collection method

In experiment 1, urine was collected using a urinary catheter. The sow was moved to a temporary cage raised approx. 1.5m, to ensure a better work environment for the person placing the catheter, making the insertion of the urine catheter safer, smoother and faster.

Figure 4.4.1 - A sow raised and having a urinary catheter inserted.

When the catheter was placed, the sow walked to its pen, and often laid down again before a stopper was placed in the catheter and time was noted. At regular intervals, the bladder was emptied in a bucket using a hose. At the end of the urine collection period, the bladder was again emptied using a hose. When no more urine was visible running though the hose, a cup was used to empty the rest. The majority of sows were lying down while emptying the bladder, but a few were standing. Very rarely a sow changed position while emptying the bladder.

In experiment 1, no sows developed urinary infection. No acids were used in the container, however, when emptying the bladder with the hose it came through a hole in the lid of the container. Only at the end, when emptying the catheter with the cup, the container was without lid.

In experiment 2, urine was collected without a catheter, having the sows in collection cages where the urine was collected in containers containing 100 ml, 5% sulphuric acid, an aliquot of 10% of the daily production was kept at 5°C until end of collection period.

In both experiments it was impossible to know when the bladder was completely empty and thereby it was also impossible to calculate the actual amount of urine

produced within a certain time frame. It was only possible to quantify the amount of urine **collected within** the given time frame. The disadvantages of collecting without a catheter, is the risk of diluting the urine with water from the water dispenser, risk of nitrogen being polluted with feces if in contact with feces, and N evaporation to the environment before the urine reaches the acid in the bucket. However as done in experiment 2 both feces, urine and gases were measured, and assuming that N is not lost in any other way, the total N collected should represented the total N excreted from the sow, while the partitioning between the different forms can be slightly different.

4.4.2. Total daily collection or 6 hours

In experiment 1, urine was collected for 6 hours, and the N output extrapolated to 24 hours. To validate this estimate, a 24-hour collection was conducted. This showed that there was reasonable agreement between estimating the total 24-hour N output from the first 6 hours collection or from 6 + 18 (24 h) collection (P=0.48; Appendix). This agrees with studies performed on pregnant women (Singhal et al., 2014).
In experiment 2 urine was collected for five days.

Table 4.4.1 Comparison between methods and time of urine collection.

	Pro	**Con**
Urinary catheter (6 hours)	Directly from bladder to container	Trained person to insert the catheter Risk of urinary infections - Emptying of the bladder is of bigger importance
No catheter (5 days)	Non-invasive	Housing in cages Risk of contamination/dilution

4.4.3. The constant used to estimate the energy content in urine

Energy in urine were calculated from the N content measured in the urine using a constant. The constant of 50.41 kJ/ g N was estimated from data used in the following two articles: Theil et al., (2002) and Theil et al., (2004). Others have found values in the same range, see Table 4.4.2.

Table 4.4.2 - Energy estimation from nitrogen content in urine.

Reference	**Method**	**Age**	**kJ / g N**[1]
Noblet et al. (2001)	Total (8 days), no catheter	18 barrows (~ 65 kg)	42.35 – 69.73
Ramonet et al. (2000b)	Total (7 days), no catheter	6 gestating sows (~ 260 kg)	44.97 – 64.22
Jaworski et al. (2016)	Total (5 days), no catheter	18 barrows (~54 kg)	40.35 – 47.93
Müller and Kirchgessner (1983)	Total (7 days), with catheter	10 sows (~190 kg)	36.01 – 41.98
Müller and Kirchgessner (1985)	Total (7 days), with catheter	12 empty sows (~ 202 kg)	35.73 – 41.45
Kirchgessner and Müller (1998)	Total (6 days), with catheter	8 empty sows (~ 182 kg)	35.08 – 35.35
Lyu et al. (2018)	Total (5 days), no catheter	18 growing pigs (~ 36.1 kg)	38.2 – 52.3
Putnam (1971)[2]	Based upon composition	Human urine	41.32

[1] Lowest and greatest between treatments in the paper

[2] Energy density values from Weast (1977) and Siderius (2017)

4.5. Heat production

Heat production (**HP**) can be estimated when all energy input and output (retention/metabolization included) has been accounted for or by measuring the heart rate. The input and output approach was used in experiment 2:

$$HP[kJ] = ME[kJ] - \left(Retained\ energy_{protein}\ [kJ] + Retained\ energy_{fat}\ [kJ]\right)$$

Where retained energy as protein and fat was estimated using the N and carbon (C) balances.

In experiment 2, HP has further been divided into activity and non-activity related heat production; this approach used the same estimates as above, except that the energy output in urine was not possible to include, as the deviation between activity and non-activity related heat production was based on four-minute collection intervals.

In experiment 1, the heart rate has been used to estimate the HP. Heart rate was measured using an activity tracker mounted on the sow, Figure 4.6.1. The Polar activity tracker was chosen, because it has previously been used in experiments with sows (Eskildsen et al., 2020b).

Initially every second sow had to be moved (those not moved would be those having heart rate measured) to avoid the neighbor sow reaching the tracker and/or belt and chew it to pieces/eat it. Both buckle and tracker on the belt were secured with plaster-tape to prevent falling off, and further the activity tracker had a clamp attached, to not being able to fall between the slatted floor if the belt and tracker would fall off. After mounting the tracker, the stable was, as far as possible, not entered by any people before taken off again.

Figure 4.5.1 - An active activity tracker mounted on a sow ready to record.

Due to it being necessary to move the sows, it was chosen only to record the heart rate between meals. Mean heart rate in the whole interval was used to calculate the HP, accordingly to Krogh et al. (2018) using the following equation: $HP\ [MJ/d] = 0.323 \left[\frac{MJ}{d}/bpm\right] \times average\ heartrate\ [bpm] - 2.4\ [MJ/d]$

Table 4.5.1 - Comparison between methods to estimate HP.

	Pro	**Con**
Energy approach	48 h measurement At the same time as other parameters are measured	Respiration chamber is required
Heart rate	Easy to mount and collect data directly from included software	Short amount of time Device not optimized for sows housed in pens Requires a model to interpret the HP Not possible the same day as other parameters are collected.

4.6. Retention

Changes in body mass was estimated in four different methods: (1) by weighing the sows, (2) BF scanning, (3) by using the deuterium dioxide (**D_2O**) technique and (4) by the difference between input and output (nutrient and energy balances).

4.6.1. Weighing and backfat

In experiment 1, each animal was weighed on the same floor scale and had the backfat measured at the same two spots, with the same Lean-Meater device (Renco Corp., Minneapolis, MN, USA), at d 0, 30, 60 and 108 in two consecutive gestating periods.

Backfat scanning was done at the P2 position (Roongsitthichai and Tummaruk, 2014). To ensure that it was possible to scan at the same spot, P2 was identified by marking the last rib, placing a measuring tape from the spine to the mark at the last rib and place a mark 6 cm down. On that mark a dot was tattooed, and thus all measurements was performed at the same spot, Figure 4.5.1. This was done on both the left and right side, and three subsequent recordings were performed on each side.

Figure 4.6.1 - Backfat scanning procedure.

4.6.2. Deuterium dioxide method

The body composition of fat and protein was calculated using the prediction equations reported by Rozeboom et al. (1994) for growing Yorkshire × Landrace gilts (approximate live weight 180 kg) and using the bodyweight of the sow, BF and analyzed D_2O space. The D_2O space was found by enrichment of 0.0425 g/kg BW D_2O solution intramuscular. Amount injected was found by weighing the syringe before and after injection. The atomic fraction prior to enrichment was analyzed using a urine sample (or blood sample in a few cases) taken prior to enrichment, while the atomic fraction after enrichment was measured by taking a blood sample 4 hours after enrichment. The D_2O equilibrium in serum is reached after approximately 2.5 h, when the D_2O solution has been injected intramuscular (Pedersen, 2019).

All sample prior to enrichment urine samples were obtained in the morning, when the sows were waking up (0-2 hours prior to D_2O enrichment). A few sows did, however, not deliver a urine sample, and in those cases a blood sample was taken before enrichment.

To be able to avoid taking the blood sample, we performed a pilot study, for the potential benefit of future studies, where urine was collected from three animals three consecutive mornings prior to enrichment (at day 28, 29 and 30 after previously being enriched). No change was observed in their atomic fraction level these three days, indicating that urine also collected 28 days after previous enrichment will have reached the lower plateau after enrichment.

The D_2O space are calculated using the following formula:

$$D_2O\ space[mole] = \frac{Injected\ D_2O\ [g]}{Molecular\ weight\ of\ injected\ D_2O[g/mol]} \times \frac{AF_{infusate} - AF_{p0}}{AF_{p1} - AF_{p0}}$$

AF, atomic fraction; p0, prior enrichment; p1, after enrichment

$$D_2O\ space[kg] = \frac{D_2O\ space[mole]\ \times\ 18.015[g/mol]}{1000[g/kg]}$$

Then the body pool of protein and fat can be estimated:

$$Body\ protein\ [kg] = 1.3 + 0.103 \times BW[kg] + 0.092\ \times\ D_2O\ space\ [kg] - 0.108\ \times BF\ [mm]$$

$$Body\ fat\ [kg] = -7.7 + 0.649 \times BW[kg] - 0.610\ \times\ D_2O\ space\ [kg] + 0.299\ \times BF\ [mm]$$

In both papers I and II, the purpose of using the D_2O dilution method was to estimate the change in the fat and protein pools. It has previously been found, that there is a detection limit of 1% in changes in the body fat pool and 0.2% in changes of the body protein pool in sows (Van Vliet et al., 2016).

4.6.3. Nitrogen, carbon and energy balances

Another way of estimating the body pool of fat and protein is to use the N balance to estimate the retention of crude protein (**CP**) (Nx6.25):

$$Total\ N\ retention\ [g/d]\ = N\ intake\ [g/d] - (Urinary\ N\ output\ [g/d] + Fecal\ N\ output\ [g/d])$$

This has been done in both experiments, however using different methods of estimating urinary N and fecal N output.

To estimate retained fat, it is necessary to measure output of both methane and CO_2, in a respiration chamber, Figure 4.5.2, as well as urinary C, fecal C and input of C, where CO_2 is the main output. Further, it is assumed that the C content of protein is

52% while it is 76.7% in fat (Brouwer, 1965). Using the following equation, the body pool of fat can be calculated:

$$Total\ fat\ retention\ [g/d] = (Retained\ C[g/d] - Retained\ N[g/d] \times 6.25 \times 0.52) \times \frac{1}{0.767}$$

This method to estimate body fat retention was used in experiment 2.

Figure 4.6.2 - A sow in a metabolic cage in the respiration chamber. Photos: Henry Jørgensen.

Fat gain can further be estimated, using the relationship between fat (from the D_2O dilution method) and backfat measurements and assuming that a change in 0.1 mm of backfat is equivalent to 346 g of fat (paper I). This comparison was done, solely with the purpose of enabling a comparison between the methods:

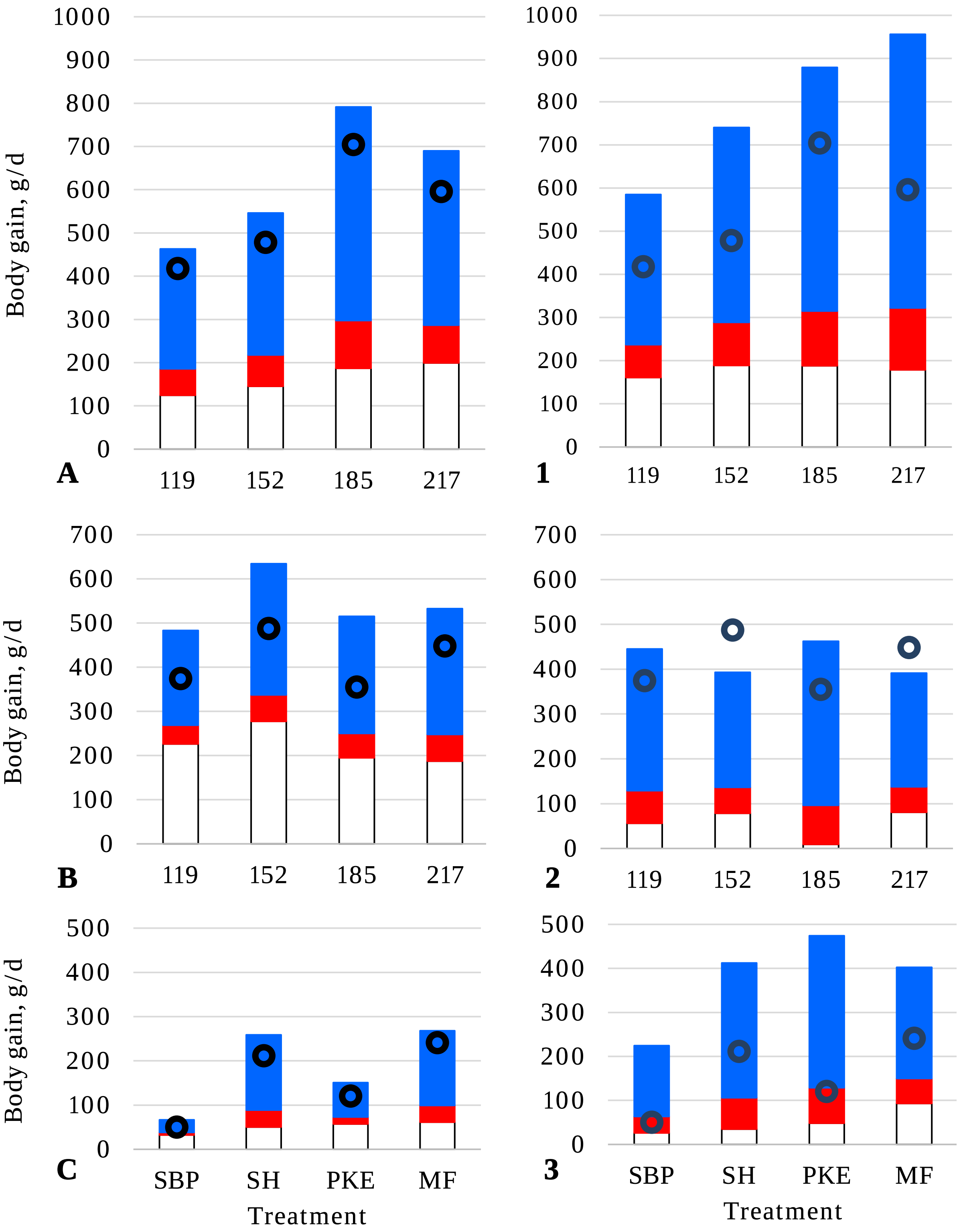

Figure 4.6.3 - Gain of fat (white bar), protein (red bar), water (blue bar), and bodyweight (black circles). Water is total bound water and minerals in both muscle and fat, assuming 4.2 g/g and 0.17 g/g, respectively (Noblet and Etienne, 1987). Letters (A-C) are calculated from the deuterium dioxide technique, while numbers (1-3) are calculated from the nitrogen balance and measured backfat, assuming 0.1 mm backfat gain are equal to 346 g of fat. A, B, 1 and 2 are from data presented in paper I, early (A and 1) and mid (B and 2) gestation, treatments are total fiber inclusion, g/kg. C and 3 are from data presented in paper II, treatments are: SBP, sugar beet pulp; SH, soy hulls; PKE, palm kernel expellers; MF: mixed fiber.

When calculating retention from balances, it is worth noticing that it is output subtracted from input and that the result will be equal to retention and errors.
In Figure 4.6.3., all retentions calculated from the N balance overestimate protein (and thereby water) compared to the retention based on the D_2O method. However, in Figure 4.6.3 (2) the total body weight gain is not overestimated at 152 and 217 g/kg of TF inclusion, which is due to the fat fraction being underestimated when comparing to the D_2O method. In general, two main causes of errors can be mentioned. Error during imprecisions in practical sampling and during analysis in the lab of both input (feed) and output (feces, urine). As an example, the overestimation of N in paper I and II is worth mentioning. In paper I and II we consider the most important error to be the lack of correct total urine collection and thereby N estimation, the bladder may not be completely empty at the end of collection, which probably leads to at least part of the N overestimation. However, it would also have been more consistent if the urine N had been analyzed using the Dumas and not the Kjeldahl method, although according to Etheridge et al. 1998, there should be no significant difference in the total N content in urine between the two methods. Both feed and feces have been analyzed using the Dumas procedure, but in different labs and this also has potential to cause variation.
Furthermore, it should be kept in mind that also extrapolations from the short balance periods to long periods of time (for example regarding urine production or heart rate measurement from only hours to a 30-day period), accumulate potential errors. This is of even greater importance in paper I and II due to the balance/collection periods being only one day. Further, in experiment I using pulse measurements obtained during only one day not even the same day as the other outputs were measured, can further add to variation when combined in the same balance.

4.6.4. Amount of feed supplied in the balance periods

When doing balances, registration of the exact feed intake is important. In experiment I, incorrect registrations of feed leftovers were not an issue since the sows emptied the through within short time. However, the exact amount of feed fed was an issue despite that an advanced automatic feeding system in the barn was used. In paper II a close look at the feed system data showed that the fed amount varied throughout the period, especially in early gestation. Due to this, we decided to use the fed amount from the morning of the sampling day and the previous afternoon feeding

0 and -1, respectively, Figure 4.6.4. In the paper the term "gestation day" has been used in table 7 instead of "average daily intake in the period", which is used in table 3.

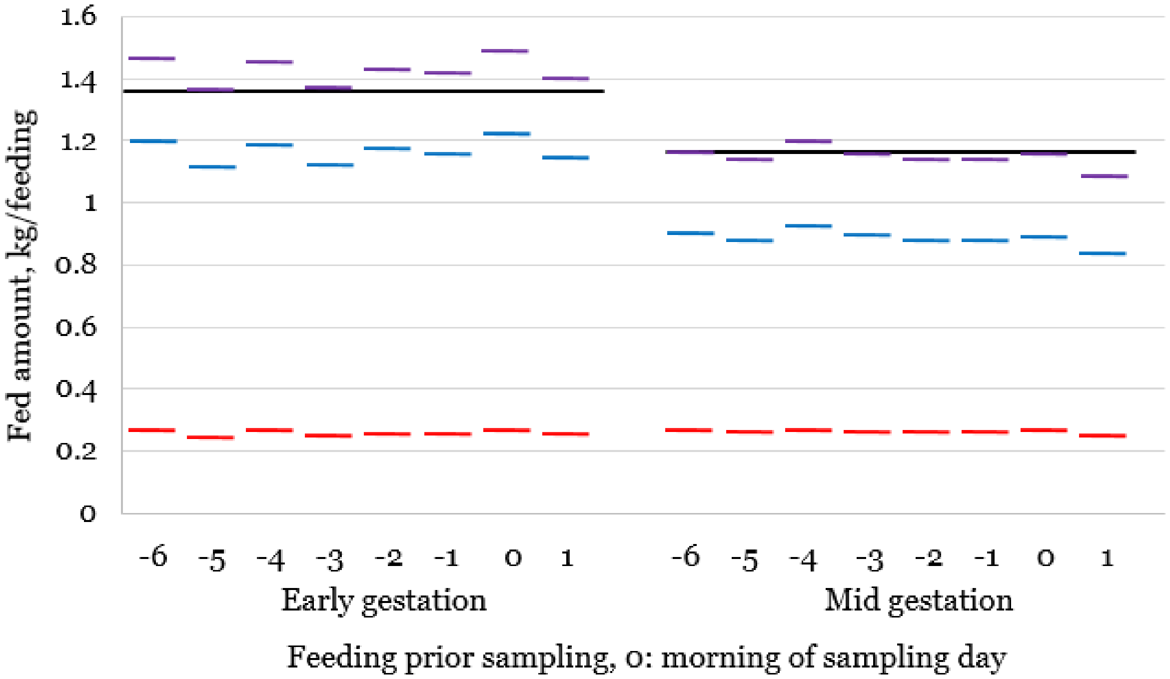

Figure 4.6.4 – A comparison between the average fed amount across 30 days (black line) and the total amount fed (purple lines) in paper II relative to the sampling day. Where 0 is the morning of the sampling day in early- and mid-gestation, respectively in paper II. Blue lines represent the amount of basal diet fed while red lines are the amount of fiber-component fed.

In paper I, the fed amount around the sampling day was similar to the average for the entire period, and therefore we chose to use the average fed amount over the period. In paper III, the feed was manually weighed and fed each day, and left overs collected, if any.

Regarding digestibility in paper II, we chose to still use the average feed fed over the period, since feed samples for chemical analysis were not obtained on the day of collecting feces (obtained every three weeks).

4.6.5. Other methods

Several other methods can be used to estimate body composition, e.g. slaughtering, 3D imaging (Le Cozler et al., 2019), air or water replacement, preferably together with lung volume measurement, Dual Energy X-Ray Absorptiometry (DXA) as well as many other methods applied in humans (Marshall et al., 2016; Kuriyan, 2018). The DXA method is also used in pigs (Mitchell et al., 2002; Strathe et al., 2019). Marshall et al. (2016) found that the best method for estimating body composition in pregnant women was the air replacement method and the authors speculated that it was superior to the D_2O technique because the women in the trial did not comply with the required fasting prior to the saliva sample collection necessary for estimating the D_2O equilibrium. Furthermore, the DXA scan, due to radiation exposure was not suitable to the group. All methods, except the slaughtering technique, require a model, like the D_2O dilution technique used here for estimating the body composition.

4.6.6. The choice of method

We chose the D_2O technique due to it being used previously in gestating sows (Eskildsen et al., 2020b), and also that many of the other techniques, e.g. as used in human medicine, require compliance from the person/animal and/or require technologies not sized for sows. The 3D technique used for cows (Le Cozler et al., 2019) does not seem to have been validated nor has a model been tested for determining the body composition of fat and protein in sows. However, it has recently been shown that 2D monitoring was capable to detect backfat changes in sows (Yu et al., 2022). Overall, body weight and backfat thickness seem more objective ways to estimate body composition, and great tool to detect changes, if repeated. Unfortunately, no model has so far been validated to quantify the body composition in the gestation period from body weight and/or backfat level.

Table 4.6.1 - Comparison between methods used to estimate fat and protein retention.

	Pro	**Con**
Deuterium dioxide dilution technique	Body pools of water, ash, fat and protein	Has limitations when gain is low Not developed for gestating sows - Require blood samples and injection of the solution
Balances (GE and N)	Non-invasive	Is the residual (including errors/uncertainty)
Balances (C)	Non-invasive	Housing in respiration chambers Is the residual (including errors/uncertainty)
Weight and backfat	Non-invasive	Backfat requires precision in repeating measurements over time. No model to quantify composition.

SECTION 5. INCLUDED PAPERS

5.1. Brief summary of paper I

Effect of different feeding strategies and dietary fiber levels on energy and protein retention in gestating sows

Wisbech, Sigrid J.; Nielsen, Tina S.; Bach Knudsen, Knud E.; Theil, Peter K.; Bruun, Thomas S.

Updated manuscript (replacement): Journal of Animal science. October 2023.

This is a retraction to:

Wisbech, Sigrid J.; Bruun, Thomas S.; Theil, Peter K.

Increased feed supply and dietary fiber from sugar beet pulp improved energy retention in gestating sows.

Published: Journal of Animal Science. 2022. 100, 1-13. Doi: 10.1093/jas/skac054

Background

The shift from glycogenic to ketogenic energy has the potential to favor fat, rather than protein deposition.

Aims

To investigate whether inclusion of increasing amount of sugar beet pulp changed the energy, protein and fat utilization in early- and mid-gestation when BF is restored.

Main results

Increased intake of sugar beet pulp decreased ATTD of both energy and N. However, due to the efficient utilization of energy in gestating sows, feed efficiency was high even at high inclusion levels of sugar beet pulp. The same was the case for N utilization and retention whereas the increase in fat deposition only was numerical. Sows fed at both low and medium feeding strategy reached the target BF level at day 108, while sows at the high feeding strategy ended at 15 mm, target BF being 16-19 mm, independent of fiber inclusion.

5.2. Brief summary of paper II

Influence of four fiber-rich supplements on digestibility of energy and nutrients and utilization of energy and nitrogen in early and mid-gestating sows.

Wisbech, Sigrid J.; Bruun, Thomas S.; Bach Knudsen, Knud E.; Nielsen, Tina S.; Theil, Peter K.

Published: Journal of Animal Science. 2023. 101, 1-13. Doi: 10.1093/jas/skad007

Background

The nutritional value of fiber-rich diets is poorly studied in sows but are of great interest due to both animal health and welfare and economically beneficial perspectives.

Aims

1) To investigate how the ATTD of nutrients was affected by inclusion of four different fiber-rich co-products; sugar beet pulp, soy hull, palm kernel expellers and mixed fiber.
2) To quantify the whole-body metabolism and utilization of energy and nitrogen when these diets were fed to sows in early- and mid-gestation.

Main results

The daily feed, nutrient and GE intake were influenced by the fiber source, with palm kernel expellers fed sows having the greatest intake and sugar beet pulp fed ones the lowest.

The ATTD of energy and nutrient except for NSP was lowest in the palm kernel expellers fed sows and highest, except for N, in the sugar beet pulp fed sows.

All four fiber-rich diets had ATTD of energy above 82% and the energy was utilized very well whereas the N utilization of all four diets were compromised.

The majority of energy was lost as heat (53% – 72%, relative to intake), whereas the majority of N was lost in urine (50% – 63%, relative to intake).

5.3. Brief summary of paper III

Influence of fiber-rich co-products on nutrient and energy digestibility and utilization in sows.

Wisbech, Sigrid J.; Nielsen, Tina S.; Jørgensen, Henry; Bach Knudsen, Knud E.

Published: Journal of Animal Science. 2023. 101, 1-10. Doi: 10.1093/jas/skad086

Background

Replacing high value grain crops with fiber-rich co-products has a great potential but our knowledge on the energy and N digestibility and utilization in sows of several fiber-rich co-products is lacking.

Aims

To quantify the energy and nutrient ATTD of six different fiber-rich co-products (Brewers spent grain, pea hull, potato pulp, pectin residue, sugar beet pulp and seed residue), and investigate the energy and N utilization in empty sows fed diets containing the fiber-rich co-products.

Main results

The ATTD of energy of the potato pulp, sugar beet pulp and pea hull diets was similar to that of the basal diet, and the ATTD of N of the sugar beet pulp and pea hull diets were similar to that of basal diet. On the contrary, the ATTD of energy and nutrients of the seed residue and pectin residue diets were relatively low, making them more suitable as gut fill rather than energy and nutrient sources.

Among the diets with the highest GE intake, seed residue, brewers spent grain and pea hull, had the lowest, intermediate and highest energy retention, respectively. This was due to their different fiber compositions, where seed residue had a low digestibility, brewers spent grain had high digestibility but also a high urinary energy output, whereas the digestibility and utilization pea hull was high. As was digestibility and utilization of sugar beet pulp. Sugar beet pulp and pea hull both has the potential to partly replace high value grain crop.

5.4. Paper I

Effect of different feeding strategies and dietary fiber levels on energy and protein retention in gestating sows

Wisbech, Sigrid J.; Nielsen, Tina S.; Bach Knudsen, Knud E.; Theil, Peter K.; Bruun, Thomas S.

Updated manuscript (replacement): Journal of Animal science. October 2023.

Running title: Dietary fiber and gestating sows

Effect of different feeding strategies and dietary fiber levels on energy and protein retention in gestating sows

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[2]Deseased

Lay summary

Feeding sows sugar beet pulp (**SBP**) has many known benefits, for example, increased satiety and high fermentability. This study investigates the ability of the sow to utilize energy for fat retention from SBP inclusions in the diet. After a demanding lactation, sows need to restore body fat, and concomitantly avoid excessive protein retention, which will increase energy demand for maintenance and risk of locomotory problems.

The hypothesis in this study is that energy from fermented fibers is more efficient for fat retention than dietary starch. In the study, sows had numerically greater fat retention when fed high concentrations of fiber from SBP, but concomitantly sows unintendedly also increased their protein retention, which in turn substantially increased their body weight. Sows were allocated to one of three feeding strategies depending on their body condition score (lean, medium or fat) in early gestation, and backfat was efficiently restored in most sows within a month.

In conclusion, although gestating sows have a high capability to utilize energy from fermentable fiber, they are disposed to protein over fat retention. These aspects need to be addressed in nutrition of modern genotype sows.

Teaser text

Increased dietary inclusion of sugar beet pulp fed to sows in early gestation enhanced numerically the fat retention and unintendedly the protein retention.

Abstract

The aim of the study was to investigate whether increased inclusion of sugar beet pulp (**SBP**) alters retention of fat, protein, and energy when backfat (**BF**) is restored in early- and mid-gestation. In total, 46 sows were fed one of four treatments with increasing inclusion of SBP providing dietary fiber (**DF**) levels of: 119, 152, 185, and 217 g/kg; sows were assigned to one of three feeding strategies (**FS**; high, medium and low) depending on BF thickness at mating and again at day 30 for the following month. On days 0, 30, 60, and 108, body weight (**BW**) and BF thickness were measured and body pools of protein and fat were estimated using the deuterium technique. On days 30 and 60, urine, feces and blood samples were collected to quantify metabolites, energy, and nitrogen (**N**) balances. On days 15 and 45, heart rate was recorded to estimate heat energy. At farrowing, total born and weight of the litter were recorded. In early gestation, BW gain ($P < 0.01$) and body protein retention increased ($P < 0.05$) with increasing fiber inclusion, while body fat retention increased numerically by 59%. Increase in BF was greatest for sows fed the high FS, intermediate when fed the medium strategy, and negligible for sows fed the lowest FS ($P < 0.001$). Nitrogen intake, N loss in feces and N balance increased linearly, whereas N loss in urine tended to decrease with increasing inclusion of fibers in early gestation. Concomitantly, fecal energy output and energy lost as methane increased linearly ($P < 0.001$), while energy output in urine declined linearly. Total metabolizable energy (**ME**) intake therefore increased from 36.5 mega joule (MJ) ME/d in the low fiber group to 38.5 MJ ME/d in the high fiber group ($P < 0.01$). Changing the ME towards more ketogenic energy was expected to favour fat retention rather than protein retention. However, due to increased intake of ME and increased N efficiency with increasing fiber inclusion, the sows gained more weight and protein with increasing fiber inclusion. In conclusion, increased feed intake improved both fat and protein retention, whereas increased DF intake increased protein retention.

Keywords: Backfat, body condition, body retention, de novo fat.feed efficiency, nitrogen utilization,

Abbreviations: ADFI, average daily feed intake; AF, atomic fraction; ATTD, apparent total tract digestibility; BF, backfat; BW, bodyweight; CP, crude protein; DF, dietary fiber; DM, dry matter; D_2O, deuterium; FS, feeding strategy; GE, gross energy; HE, heat energy; ME, metabolizable energy; NEFA, non esterified fatty acid; N, nitrogen; NSP, non starch polysaccharide; RE, retained energy; RF, retained (body) fat; RFE, retained fat energy; RP, retained (body) protein; RPE, retained protein energy; SBP, sugar beet pulp; SCFA, short chain fatty acid; TiO_2, titanium dioxide

Introduction

A challenge in practical pig production is to control the body condition of sows throughout the reproductive cycle. Hyperprolific sows mobilize substantial amounts of body fat for the demanding milk production (Krogh et al., 2017; Strathe et al., 2017), and it is essential to restore lost body fat and protein during the following gestation period.

Fat deposition occurs when animals ingest excess energy, but the genetic selection has favored protein accretion over fat accretion in modern pig breeds. Energy in a normal diet for gestating sows mainly derives from glucose from digested starch, which can be used for either oxidation or de novo fat synthesis. Amino acids may be used as energy also, but are prioritized for protein accretion, and this process is also fueled by glucose oxidation. Fibers are fermented in the hindgut, and energy is taken up as short chain fatty acids (**SCFA**), mainly as acetate, propionate and butyrate. Ketogenic substrates, acetate and butyrate, are more suitable for de novo fat synthesis than glucose, because two of six carbons from glucose is lost as CO_2 when glucose is the precursor for de novo fat synthesis (Theil et al., 2020), whereas all carbons in acetate and butyrate can be utilized. The Danish energy evaluation system for pigs focus on the potential energy value of feed stuffs when nutrients are oxidized (Kil et al., 2013). However, it does not take into account that within the body carbon is utilized much more efficiently (100% for SCFA vs. 67% for glucose) when digested nutrients are used as precursors for de novo synthesized fat.

Dietary fibers (**DF**) have a wide range of beneficial effects. For instance, more fibers decrease the diurnal variation in energy being net absorbed to portal blood, because uptake of SCFA is fairly constant during the post prandial period, whereas net absorption of glucose peaks approximately 60 min after feeding and then decline (Serena et al., 2009). Dietary fibers are also known to reduce physical activity (Rijnen et al., 2001), aggression, stress and stereotypic behavior (Priester et al., 2020), and especially in early gestation, these are risk factors for early embryonic mortality (Peltoniemi et al., 2021). Housing animals individually or in uniform groups also limits these risk factors (Peltoniemi et al., 2016), which further gives the opportunity to feed strategically to reach a certain target of backfat (**BF**). Understanding the importance of feed level and feed composition for muscle and fat retention of gestating sows is important when taking sow productivity, feed efficiency, health and welfare into account.

The hypothesis in the current study was that adding fiber to the diet would improve energy utilization of sows when restoring BF, due to improved carbon (energy) utilization, reduced physical activity and reduced heat loss.

Materials and methods

The present experiment complied with the Danish ministry of Justice Law number 382 (June 10, 1987), Act number 726 (September 9, 1993, as amended by act number 1081 on December 20, 1995), concerning experiments with the care of animals. The Danish Animal Experimentation Inspectorate approved the study protocol (License number: 2018-15-0201-01484).

Animals and housing

A total of 46 multiparous hybrid sows (DanBred landrace x DanBred Yorkshire) were stratified for BF thickness and body weight (**BW**) at weaning and allocated to four different treatments. The experiment was carried out in 2 blocks of 25 and 21 sows.

Animals were housed individually until day 60, in crates (65cm x 245 cm) with partly slatted floor. From day 60, sows were group housed until entering the farrowing unit around day 108. When group housed, single crate with feed trough were used voluntary by the sows, feeding were supervised with the possibility to lock the crates, to ensure enough time for each sow to eat the meal.

The temperature was kept constant at 18 °C and the light were turned on 18 hours each day. Water intake was not monitored. The trial was conducted at Aarhus University, Foulum.

The sows were inseminated with mixed Duroc (DanBred Duroc, Hatting Agro, DK-8700 Horsens, Denmark) semen.

Experimental design, dietary treatments and feeding

Two diets (low and high fiber) were formulated based on wheat, barley and soybean meal, and SBP partly replaced wheat in the high-fiber diet (**Table 1**). Both diets were formulated to contain the required amounts of nutrients per unit of net energy according to Danish recommendations for gestating sows (Tybirk et al., 2020). These two diets were produced by Vestjyllands Andel (DK-6950 Ringkøbing, Denmark), and at the experimental facility at Aarhus University, two additional treatments (33 % low/67% high and 67% high/33% low DF diets) were mixed before each feeding from the low- and high-fiber diets to achieve an increasing gradient with DF.

The animals were fed two times every day (0900 h and 1400 h), and feed leftovers, if any, were collected. Titanium dioxide (**TiO_2**) was added to the diet as a marker to quantify the digestibility of nutrients. All sows were fed the allocated diet until they were moved to the farrowing unit at d 108.

Feeding strategy. Sows were allocated to one of three feeding strategies (**FS**), depending on their BF level (SEGES Innovation, Denmark) at mating; High FS (<13 mm), medium FS (13 to 16 mm) and low FS (>16 mm) and the FS for individual sows was re-considered using the same criteria at d 30. From day 60 and onwards, all animals were fed the same FS. The feed was supplied according to Danish feed units for sows, which are closely related to net energy basis (Patience, 2012). Converting to metabolizable energy (**ME**), the high FS sows were fed 55.4 ME/d from day 0 to 30, medium FS sows were supplied 36.9 ME/d and low FS sows 30.8 ME/d. From day 31 to 60, high FS sows were fed 36.9 ME/d, medium FS sows 32.0 ME/d, and low FS sows 27.1 ME/d. From day 61 to 84, all sows were fed 32.0 ME/d and from d 85 to 108, all sows were fed 43.1 ME/d.

Experimental procedure

The experiment consisted of two periods with detailed studies, of which day 0 to 30 represent early gestation and day 30 to 60 represent mid-gestation. The subsequent third period, late gestation, focused only on feed intake and changes in BF; BW and body composition.

Sampling. The animals were weighed, and BF scanned at day 0, 30, 60 and 108.

Backfat scannings were performed using Lean-Meater (Renco Corp., Minneapolis, MN) at the last rib and 6 cm from the spine, known as P2 BF. A dot was tattooed to ensue repeated measurements were carried out at the same spot at each subsequent sampling. Mean value of six scannings (three on each side) were used to record the BF.

Blood was drawn 4 h after feeding by puncturing the jugular vein at day 0 (only serum), 30 and 60. About 9 mL of blood was collected for harvesting plasma in heparinized vacutainer tubes (Grein Bio-One, GmbH, Kremsmünster, Austria) the plasma was stored on ice until centrifuging. Moreover, 4 mL of blood was collected in vacutainers without anticoagulant, which were left to clot for a minimum of six hours before centrifugation and harvest of serum. All samples were centrifuged for 10 min at 1558 × *g* at 4 °C. Plasma and serum samples were stored at -20°C for later analysis.

Deuterium (D_2O) enrichment. On days 0, 30, 60 and 108 the D_2O technique was used to assess body pools and of fat and protein according to Rozeboom et al. (1994), which were used to calculate the retention of fat and protein. The D_2O space in sows was measured as described by Theil et al. (2002b). To determine the D_2O background level, a urine sample was taken prior to enrichment and stored at -20°C. Enrichment was done, just before feeding, intra muscularly in the neck or thigh (1S8G, 40-mm needle, 10-mL syringe) with a 40% deuterium oxide (Sigma-Aldrich, MO) and 60% saline (9-mg NaCl/mL; B. Braun Melsungen AG, Melsungen, Germany) solution, by injecting 0.0425 g solution per kg live weight. The serum sample was collected 4 hours after feeding and enrichment, when D_2O was equilibrated with body water.

Urine and fecal samples. Feces and urine samples were collected at day 30 and 60. A fresh fecal sample was collected and frozen for further analysis. Urine was collected for 6 hours during the day time using a urinary balloon catheter (Teleflex medical, Kamunting, Malaysia). A stopper in the catheter ensured urine stayed inside the urinary bladder, which was emptied every second hour into a contained, which was immediately closed with a lid and kept cold until collection was completed. The amount of urine was registered, and a pooled subsample was stored at -20°C until analysis.

The heart rate was measured at day 15 and 45 for four consecutive hours, initiated when all sows had completed their morning meal, with a tracking system (Polar Team Pro GPS tracking system, Polar, Ballerup, Denmark) mounted on an elastic band, which were fitted around the belly of the sow just behind the front legs.

Representative feed samples were collected every third week and stored at -20°C and pooled prior to analysis.

Chemical analysis

Feed and feces. Both feed and fecal samples were analyzed for dry matter (**DM**), ash, total non starch polysaccharides (**NSP)**, nitrogen (**N**), gross energy (**GE**) and TiO_2, and feed was also analyzed for Klason lignin. Feed samples were analyzed for amino acids, N, crude fat, vitamins and minerals according to the Official Journal of the European Union (EU; 152/2009). Starch, total, soluble and insoluble NSP and Klason lignin were analyzed according to Bach Knudsen (1997). Gross energy was determined in an Automatic Isoperibol Calorimetry system (Parr Instrument Company, Moline, Illinois, USA).

Nitrogen was analyzed according to the Dumas method (Hansen, 1989) using a Vario Max CN Element analyzer (Elementar Analysensytem GmbH, Langenselbold, Germany) aspartic acid were used as a calibrating standard. The concentration of crude protein (**CP**) was calculated as Nx6.25.

The concentration of TiO_2 was analyzed in diets in duplicate, and in feces as single analysis as described by Short et al. (1996).

Plasma and urine. To determine plasma concentrations of glucose, lactate, triglycerides and urea, standard assays from Siemens Diagnostics (Siemens Diagnostics Clinical Methods for ADVIA 1650) were applied and quantified using an auto analyzer (ADVIA 1650 Chemistry System, Siemens Medical Solution, Tarrytown, NY). Non esterified fatty acid (**NEFA**) was determined using the Wako, NEFA C ACS-ACOD assay method (Wako

Chemicals GmbH, Neuss, Germany) and quantified using an auto analyzer (ADVIA 1650 Chemistry System, Siemens Medical Solution, Tarrytown, NY). The content of N in urine was determined by the Kjeldahl method (Method 984.13; AOAC Int. 2000) using a KjelTecTM 2400 (Foss, Hillerød, Denmark). The denoted atomic fraction (**AF**) of the D_2O space was measured by isotopic ratio mass spectrometry (Delta S; Finnigan MAT, Bremen, Germany), after ultrafiltration and reducing to free hydrogen, as described by Theil et al. (2002b).

Calculations and statistical analysis

Deuterium. From the AF D_2O enrichment in infusate and in urine before (AF_{P0}) and in serum after enrichment (AF_{P1}) the D_2O space was calculated, as:

$$D_2O\ space[mole] = \frac{Injected\ D_2O\ [g]}{Molecular\ weight\ of\ injected\ D_2O[g/mol]} \times \frac{AF_{infusate} - AF_{p0}}{AF_{p1} - AF_{p0}},$$

$$D_2O\ space[kg] = \frac{D_2O\ space[mole] \times 18.015[g/mol]}{1000[g/kg]},$$

The body pools of protein and fat were then calculated based on formulas for Yorkshire × Landrace gilts as reported by Rozeboom et al. (1994):

$$Body\ protein\ [kg] = 1.3 + 0.103 \times BW[kg] + 0.092\ \times\ D_2O\ space\ [kg] - 0.108\ \times BF\ [mm]$$

$$Body\ fat\ [kg] = -7.7 + 0.649 \times BW[kg] - 0.610\ \times\ D_2O\ space\ [kg] + 0.299\ \times BF\ [mm]$$

Retention of body protein (**RP**) and fat (**RF**) was then calculated as:

$$Retention[kg/d] = \frac{(Final\ body\ pool\ [kg] - initial\ body\ pool\ [kg])}{Days}$$

Retained energy (**RE**) was calculated using the data obtained using the D_2O method, assuming that 1 kg of protein and fat corresponds to 23.9 MJ and 39.8 MJ, respectively (Theil et al., 2020):

$$RE = RP[kg] \times 23.9\ [MJ/kg] + RF[kg]\ \times 39.8\ [MJ/kg]$$

Similarly, retained energy as protein (**RPE**) and retained energy as fat (**RFE**) was calculated using the same energetic constants and expressed relative to realized ME intake.

Digestibility. Digestibility of nutrients were measured as apparent total tract digestibility (**ATTD**) using TiO_2 as a marker, and calculated (with N used as example) as follows:

$$ATTD\ N\ [\%] = 100 - \left(100\ \times \frac{Diet\ TiO_2\ [\%]}{Fecal\ TiO_2\ [\%]} \times \frac{Fecal\ N\ [\%]}{Diet\ N\ [\%]}\right)$$

An average of TiO_2 in each batch was used to calculate digestibility for each specific sow and day.

Nitrogen balances. The N balance was calculated as N intake minus urinary and fecal N outputs, as follows:

$$Total\ N\ retention\ [g/d]\ = N\ intake\ [g/d] - (Urinary\ N\ [g/d] + Fecal\ N\ [g/d])$$

Energy balances. Retained energy (RE$_{GE}$) was calculated as GE intake minus urine GE, fecal GE, energy lost in methane and total heat energy (**HE**) as described below:

$$Urine\ GE\ [MJ/d] = \frac{Urine\ N\ [g/d] \times 50.4\ [kJ/g]}{1000\ [kJ/MJ]}$$

It was assumed that urine contained 50.4 kJ per g of N (Theil et al., 2002a, 2004), and that N lost through urine during 6 h was representative of the daily output.

Gross energy in methane was calculated, according to Jørgensen et al. (2011) using the digestibility and content of NSP in the feed:

$$Methane\ GE\ output[MJ/d] = \frac{0.0628 + 0.00488 \times \left(\mathrm{NSP}[g/kg\ DM] \times \frac{ATTD\ NSP\ [\%]}{100}\right)}{100} \times GE\ intake\ [MJ/d]$$

The HE was calculated according to Krogh et al. (2018), using the mean heart rate recorded:

$$HE\ [MJ/d] = 0.323 \left[\frac{MJ}{d}/bpm\right] \times average\ heartrate\ [bpm] - 2.4\ [MJ/d]$$

then, the RE$_{GE}$ was calculated as follows:

$$RE_{GE}[MJ/d] = GE_{Intake}[MJ/d] - (Fecal\ GE\ output[MJ/d] + Urine\ GE\ output[MJ/d] + CH_4E\ output\ [MJ/d]\ + HE[MJ/d])$$

Statistical analysis

The statistical analysis was performed using a MIXED model in the SAS software (version 9.4, SAS Institute Inc., Cary, NC, 2012). The following model was applied to analyze all data:

$$Y_{ijk} = \mu + \alpha_i + \beta_j + \tau_k + \varepsilon_{ijk}$$

Where Y_{ijk} is the response variable, μ is the overall mean, α_i is the fixed effect of treatment (0%, 33%, 67% and 100% inclusion of the high-fiber diet), β_j is the fixed effect of feeding strategy (high, medium and low), τ_k is the random effect of block (1 and 2) and ε_{ijk} is the residual error component, which was assumed to be normally distributed N $(0, \sigma^2)$. Within the model, analysis of variance (ANOVA), linear effect for dietary treatments was tested, whearas FS was only tested using the ANOVA. Mean values are presented as least square means ± SEM, where the highest SEM for treatment and FS, respectively, are shown. Effects were considered significant at $P \leq 0.05$ and as tendencies when $0.05 < P \leq 0.10$. Interaction between DF and FS were tested, but none were found significant and hence not reported.

Results

Dietary treatment

The DF increased from 119 g/kg in the low-fiber diet to 217 g/kg in the high-fiber diet, and concomitantly the calculated dietary content of ME decreased from 13.5 MJ/kg in the low-fiber to 12.7 MJ/kg in the high-fiber diet. The CP content increased 4% from 115 g/kg in the low DF diet to 120 g/kg in the high DF diet, while lysine decreased by 7% from 5.47 g/kg to 5.09 g/kg (**Table 2**).

Feeding strategy

On days 30, 12 sows were moved from the high to the medium FS, six sows from the medium to the low FS, 2 sows from the high to the low FS, 1 sow from the low to the medium FS, and the remaining sows stayed at the same FS as in early gestation. As a consequence, only two sows were fed the high feeding strategy in mid-gestation, and due to the low number in that treatment group, they were omitted in the statistical analysis for mid-gestation (d 30 to 60).

Digestibility

With increasing fiber levels, the digestibility of DM, N, GE, and organic matter decreased linearly in early gestation while digestibility of NSP increased linearly ($P < 0.001$; **Table 3**). The same pattern was observed in mid-gestation ($P < 0.05$) although no evidence of a dietary effect on DM digestibility was observed. Digestibility of NSP increased linearly with increasing fiber inclusion in both gestation periods ($P < 0.001$). The FS did not affect digestibility of nutrients, except digestibility of NSP, which tended ($P = 0.06$) to be higher in sows fed the medium FS as compared with sows fed the low FS in mid-gestation.

Sow performance and feed utilization.

In early gestation BF (due to the experimental design) but also BW, body protein and body fat differed and were all lowest in the high FS group, intermediate in the medium FS group and highest in the low FS group (**Table 4**). The average daily feed intake (**ADFI**) in early gestation increased linearly from 2.83 kg/d in the low-fiber diet to 3.07 kg/d in the high-fiber diet, and concomitantly the fiber intake increased from 346 g/d to 662 g/d ($P < 0.001$). The fiber intake also increased in mid-gestation ($P < 0.001$). The intake of ME did not differ among the dietary treatment groups neither in early- nor in mid-gestation. In both early- and mid-gestation, ADFI, energy intake and fiber intake were highest in sows fed the high FS, intermediate in the medium FS and lowest in the low FS group ($P < 0.001$).

In early gestation, BW gain ($P < 0.01$) and RP ($P < 0.05$) increased linearly with increased fiber inclusion, and RF increased 59% (from 0.125 to 0.199 kg/d) although that change was not statistically significant. In mid and late gestation, no differences in BW gain, BF gain, RP and RF were observed across the dietary treatments. In early gestation, sows fed the high FS had the greatest increase in BF, sows fed the medium FS had a lower increase in BF and sows fed the low FS hardly gained BF in this period. From mating until sows entered the farrowing unit (d 108), sows gained 4.1, 2.6, and 1.4 mm in BF, respectively (**Fig. 1**), when considering the feeding strategies applied from d 0 to 30. Body weight gain to feed ratio and RP to feed ratios were lowest in the low fiber treatment and increased linearly with increasing DF ($P < 0.05$) in early gestation. Retained protein energy as percentage of ME_{Intake} were greatest when including 185 g DF/kg (7.2%) compared to 3.7% when no SBP were included ($P < 0.05$). In early gestation, the high FS had the highest BW, BF and RF to feed ratio ($P < 0.001$) and RP to feed ratio ($P < 0.01$).

Metabolites

In both early- and mid-gestation, plasma urea decreased linearly when fiber intake increased ($P < 0.05$; **Table 5**). The plasma NEFA was highest ($P < 0.01$) in both early and mid-gestation in sows fed the low FS, and plasma urea was highest in sows fed the high FS in early gestation ($P < 0.001$), while no difference was observed in mid-gestation for plasma urea.

Balances of N and GE

N intake, N loss in feces ($P < 0.001$; **Table 6**) and total N retention ($P < 0.05$) increased linearly with increasing fiber intake in early gestation. Expressed relative to N intake, fecal N output only accounted for 18 % to 22 % in the low- and high-fiber diets, respectively, N lost through urine decreased from 59 % to 38 %, and N retention increased from 23 % to 39 % with increasing inclusion level of fiber (**Fig 2A**). In mid-gestation, N intake ($P < 0.05$) and fecal N output ($P < 0.001$) increased linearly with increasing fiber intake, whereas total N retention and urinary N loss did not differ across treatments.

Heart rate tended to decrease in mid-gestation in response to increased fiber levels ($P=0.06$), and the same pattern was observed in early gestation, although there was no statistical evidence of a dietary response.

In early gestation, the GE intake, fecal GE output and methane GE output increased linearly ($P < 0.001$) with increasing fiber levels. The total ME increased with increasing fiber inclusion from 36.5 MJ/d in the low-fiber diet to 38.5 MJ/d in high-fiber diet ($P < 0.001$). In mid-gestation, fecal and methane GE output increased linearly ($P < 0.05$), while HE tended to decrease linearly with increasing fiber inclusion ($P = 0.06$) giving rise to a tendency of increased total energy retention from -2.5 MJ/d in the low-fiber diet to 2.1 MJ/d in the high-fiber diet ($P = 0.07$). Regarding FS in early gestation, GE intake, fecal GE output, methane

GE output, ME, and total energy retention ($P < 0.001$) were highest in the high FS, intermediate in the medium and lowest in the low FS group. In mid-gestation, GE intake, Fecal GE output, methane GE output, ME ($P < 0.001$) and urine GE output ($P < 0.05$) were highest in medium FS and lowest in low FS while retained energy did not differ between FS. The realized dietary ME did not differ across dietary treatments and amounted to 12.6 to 12.9 MJ ME/kg feed in both early- and mid-gestation.

Discussion

Restoring body condition

High feed intake restored BF in sows with inadequate BF almost to the targeted level (16 to 19 mm BF), while a low feed intake maintained the BF level fairly constant in sows that had adequate BF at mating. Thus, restoring BF by adjusting the feeding level was successful, as the sows fed the high feeding level rapidly increased their BF in early gestation (+2.6 mm from d 0 to 30 and +4.1 mm during the entire gestation), while fat sows fed the low feeding strategy gained least BF (+0.3 mm from d 0 to 30 and +1.4 mm during the entire gestation). This is in line with Young et al. (2004) who found that feeding according to BF thickness resulted in more sows ending up within their target zone (17 to 21 mm BF in their study) at farrowing as compared with visual scoring of body condition. This is also supported by Maes et al. (2004), who found that BF measurements and visual scoring were only moderately correlated. In Denmark, it is common to differentiate the FS depending on BF level at mating and supply feed within the range of 2.2 to 4.3 kg/d from day 0 to 30 with the overall aim of reaching 16 to 19 mm of BF when sows enter the farrowing unit around d 108 (Pedersen, 2020). On day 30, the recommended feed supply was lowered for all FS as compared with early gestation to attenuate retention of BF. From day 60 until 84 of gestation, it is recommended to supply all sows with 2.2 kg/d, and from d 85 and up until sows enter the farrowing unit, the feed supply should be kept constant at 3.3 kg/d (SEGES, 2019). In the current study, reduced variation in BF was observed with progress of gestation but unfortunately the high FS group barely reached the range of 16 to 19 mm BF. Increasing the level of DF from 119 to 217 g/kg by increasing the inclusion level of SBP increased the BW gain linearly from 417 to 596 g/d, and the body fat retention of sows by 59% (from 125 to 199 g/d) based on the D_2O dilution technique, although the latter did not differ significantly. Increasing the DF concentration at the expense of decreased starch increased the uptake to the portal vein of ketogenic energy metabolites, acetate and butyrate at the expense of glucose (Serena et al., 2009). These ketogenic metabolites are precursors that can directly be utilized in *de novo* fat synthesis in anabolic sows (Theil et al., 2020). Therefore, DF most likely favor body fat accretion. In contrast to our expectation, the body protein retention and sow BW gain increased linearly with increasing DF concentration in early gestation. In the lactation period prior to this study, the sows lost on average 8% of their BW, 2% of their body protein pool and 16% of their body fat pool (Bruun et. al., 2023). Hence the observed protein retention seemed not to be driven by a pronounced need for restoring lost body protein. Two explanations seem to be plausible for the fiber effect on protein retention. One option is that sows fed increasing amounts of fiber ingested more ME, which normally is the limiting factor for protein retention in gestating sows (Dourmad et al., 2008). Another option is that increasing the proportion of energy originating from fiber at the expense of starch attenuates the diurnal fluctuations in energy uptake from the gastrointestinal tract (Serena et al., 2009) thereby improving the utilization of dietary amino acids and CP and, unintendedly, increase lean growth instead of fat retention. Both mechanisms may well have contributed to altering the feed utilization in the sows in the present study and blurred the dietary responses on restored body fat and BF across the four dietary treatments.

Fiber and HE

Heat energy is influenced by many factors, including live weight, feed intake, feed composition, ambient temperature, stage of gestation and physical activity (Brouns et al., 1994; Theil et al., 2020). It is indeed a challenge to quantify the HE of gestating sows, because physical activity is confined when studied in respiration chambers (Jakobsen et al., 2005). In the current study, the mean heart rate recorded during a 4-h period after completion of the morning meal was used to estimate the daily HE. According to the recorded mean heart rate, the study suggested that the HE could be 7% (NS) and 16% ($P = 0.06$) lower in early- and mid-gestation, respectively, when comparing the low- and high-fiber diets. In agreement with this, Rijnen et al. (2003), reported that group housed sows had decreased HE when they were fed high levels of SBP. On the other hand, Olesen et al. (2001) reported a numerically greater HE in sows fed a high-fiber mix diet (with fibers originating from SBP, oats, grass pellets and wheat bran). The higher HE reported for the high-fibre diet reported by Olesen et al. (2001) is in agreement with the theoretical held framework that the handling of a more bulky digesta will require more energy. However, in the case of SBP this effect may be overshadowed by a higher energy efficiency of absorbed SCFA (acetate, propionate, butyrate) originating from fermentation of fibers in the hindgut compared to glucose from starch. The SCFA give raise to less heat when utilized for de novo fat synthesis as compared with glucose, because of more steps in the metabolic pathway for glucose than for ketogenic

SCFA. Thus, 2 of 6 carbons (33%) and 14 of 38 adenosine triphosphate (37%) are lost and correspondingly additional heat is generated when glucose is converted into two molecules of acetyl Coenzyme A (Theil et al., 2020). In contrast, no carbons are lost (and less heat is produced) if acetate or butyrate are precursors for de novo fat synthesis. These aspects are not taken into account in the Danish energy evaluation system because the system only consider the potential energy value of digested nutrients under the assumption that they are completely oxidized. Another reason why HE decreased with increasing fiber inclusion may be due to fermentation heat from the hindgut, which supply extra intrinsic heat to the sow and possibly reduces the need for HE due to thermoregulation. This is, however, mostly relevant for sows fed around (or below) maintenance, whereas sows fed well above maintenance (e.g. to restore BF) produce so much additional heat due to the anabolic processes that no nutrients needs to be oxidized for thermoregulatory purposes. In line with the latter explanation, Ramonet et al. (2000) explored the partitioning of HE between a combined fiber source and a control diet in gestating sows fed around maintenance. In the study, they reported that the thermic effect of feeding (i.e., increased post prandial HE due to digestion processes) increased when feeding a fiber rich diet (Ramonet et al., 2000). To fully understand and differentiate the heat production between maintenance, anabolic processed and fermentation processes, further studies are needed, especially with focus on fat retention.

Fiber and energy balance in early- and mid-gestation

Total energy retention tended to increase linearly with the inclusion of SBP to the diet in mid-gestation (from d 30 to 60) and the same pattern was observed in early gestation, although no statistical difference was observed. This effect was primarily due to increased intake of ME combined with decreasing energy lost as heat. This is in line with Rijnen et al. (2001), who found a constant total energy retention, in spite of a decrease in ME intake. All groups of sows in the present study metabolized the energy that was expected based on the dietary formulation. The sows metabolized 12.9 MJ ME/kg and 12.6 MJ ME/kg in the low- and high-fiber diet in early gestation, respectively, which was close to what was expected based on the Danish feed evaluation system (13.5 MJ/kg and 12.7 MJ/kg respectively).

A benefit of achieving a correct energy value of the sow diets is that the protein (i.e., amino acids) to energy ratio are as close as possible to the National nutrient recommendations (Tybirk et al., 2020). Underestimating the energy value in sow diets can lead to increased protein and fat retention and hence unintended weight gain, which in turn increases the energy requirement for maintenance throughout the remaining life of the sow. Moreover, it may lead to increased risk of overloading the joints with potential consequences on reproductive performance (Prunier et al., 2010) and reduced longevity (Jorgensen and Sorensen, 1998). Increased energy intake, even when provided as energy as in the current study, can increase the protein retention.

Plasma NEFA is a good indicator of the energy balance of the animal (Ren et al., 2017), as also reflected by the decreased NEFA with increasing feed intake across feeding strategies. In the current study, the plasma NEFA concentration was not affected by the inclusion level of SBP, which supported the lack of difference of different fiber levels on energy retention.

Fiber and impact on feed efficiency and productivity

Sugar beet pulp, compared to other fiber sources, is highly fermentable and thus a well suited fiber source for gestating sows, as it contains high levels of pection (uronic acids) and low levels of lignin (Bach Knudsen, 1997). Moreover, SBP is characterized by a high water binding capacity (Zhou et al., 2018), which increases the gut fill. A high water binding capacity increase the surface area of the feed matrice in the gastrointestinal tract, allowing easier access for microbial enzymes to reach their substrates in the hindgut (Renteria-Flores et al., 2008; Priester et al., 2020). In the current study, digestibility of GE and all nutrients except NSP decreased with increased amount of SBP. This is a consequence of the high ratio of soluble compared to insoluble NSP (Burkhalter et al., 2001) and in agreement with studies of Olesen et al. (2001) and Renteria-Flores et al. (2008) that also showed higher fermentability of fibres in SBP compared with other fiber sources like wheat bran and wheat straw (Renteria-Flores et al., 2008).

In spite of decreasing digestibility of both energy and N, the feed efficiencies were higher when more fibers were included in the diet. That the protein gain per kg feed (from d 0 to 30) increased from 119 to 185 g DF/kg emphasizes that the sows ability to utilize both N and energy was highly efficient even at high inclusion levels of SBP.

Both a higher energy intake and indication of a more stable diurnal uptake of energy, especially in early gestation may well affect farrowing parameters as total born, because the energy balance influences the embryonic mortality (Zhou et al., 2019; Peltoniemi et al., 2021). In the current study, inclusion of SBP tended to increasethe number of total born piglets, which corroborated the findings of van der Peet-Schwering et al. (2003) who found an increase of 0.5 total born piglets when sows were fed a high-fiber diet throughout three parities. On the other hand, Danielsen and Vestergaard (2001) did not find any impact of feeding a low-fiber control diet or a high-fiber diet based on SBP on number of total born piglets, but they reported a lower mean piglet birth weight in sows fed the high-fiber diet. More recently, a large Danish study with 3,163 sows did not report any impact on total born when comparing a diet high in SBP (450 g SBP/d on average) with normal gestation feed (Sørensen et al., 2016). The observed increase in total born piglets with increased inclusion of fiber in the present study could also be explained by the increased energy intake in early gestation. In line with that, Hoving et al. (2011) found an increased litter size in sows fed additional 30 % energy during the first 30 days of gestation as compared with no additional energy or additional 30 % energy from dietary protein (Hoving et al., 2011). The present study clearly indicate that high levels of DF have no negative consequences for reproductive output, whereas it is more questionable whether the fibers indeed had a beneficial effect.

Fiber and protein utilization

The N retention increased with increasing fiber, mainly because N intake increased while the urinary N output decreased. As a consequence, N efficiency for retention increased with inclusion of fiber from 23% to 39% in early gestation. In line with this, Yang et al. (2021) found that N efficiency increased from 41% to 50% when adding a fiber mixture to a low fiber control diet in early gestation. The altered N metabolism towards less N loss in urine and more loss via feces in response to increasing DF was, apart from lower N digestibility, most likely also due to greater recirculation of urea from the blood to the intestinal lumen (Jarrett and Ashworth, 2018; Yang et al., 2021). In line with this, Yang et al. (2021) found that 60 to 80% of total N in feces was microbial protein N and that inclusion of fiber increased the amount of microbial protein, indicating a greater population and likely also greater diversity of the microbiota in response to fiber inclusion.

Conclusion

This study showed that gestating sows efficiently utilize energy from SBP and that increasing levels of DF improved the N retention and N utilization. Concomitantly a numerical improvement in fat retention was observed. This emphasizes the importance of understanding energy utilization within the animal to be able to formulate the dietary composition correctly taking the energy value of feedstuffs into account. In future studies it would be recommendable to focus on interactions between DF and FS and between DF and dietary protein sources, as they may affect the nutrient absorption dynamics.

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Disclosure

All authors declare that there are no conflict of interest

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Figure 1

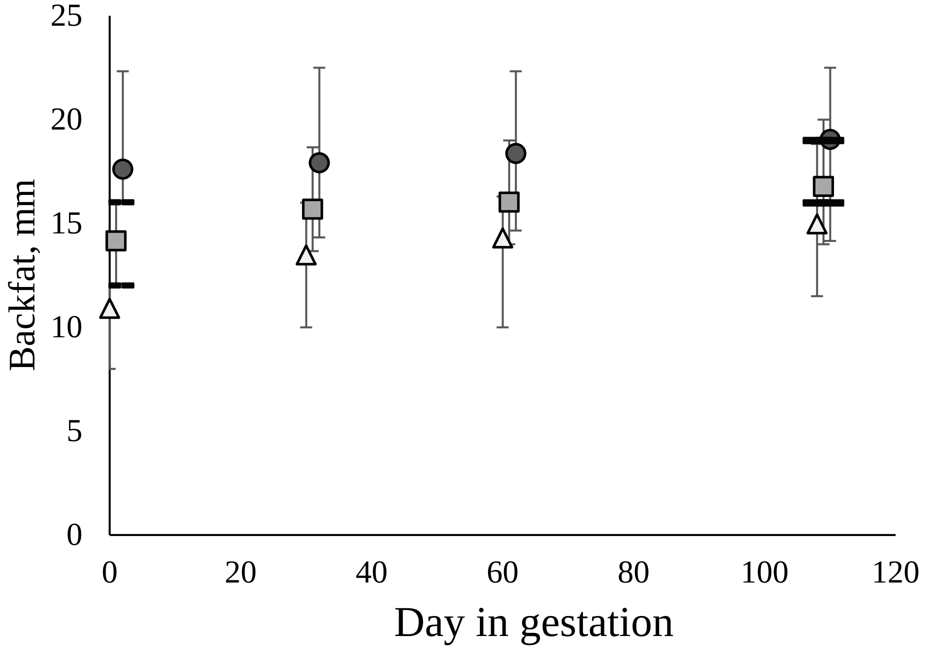

Figure 2

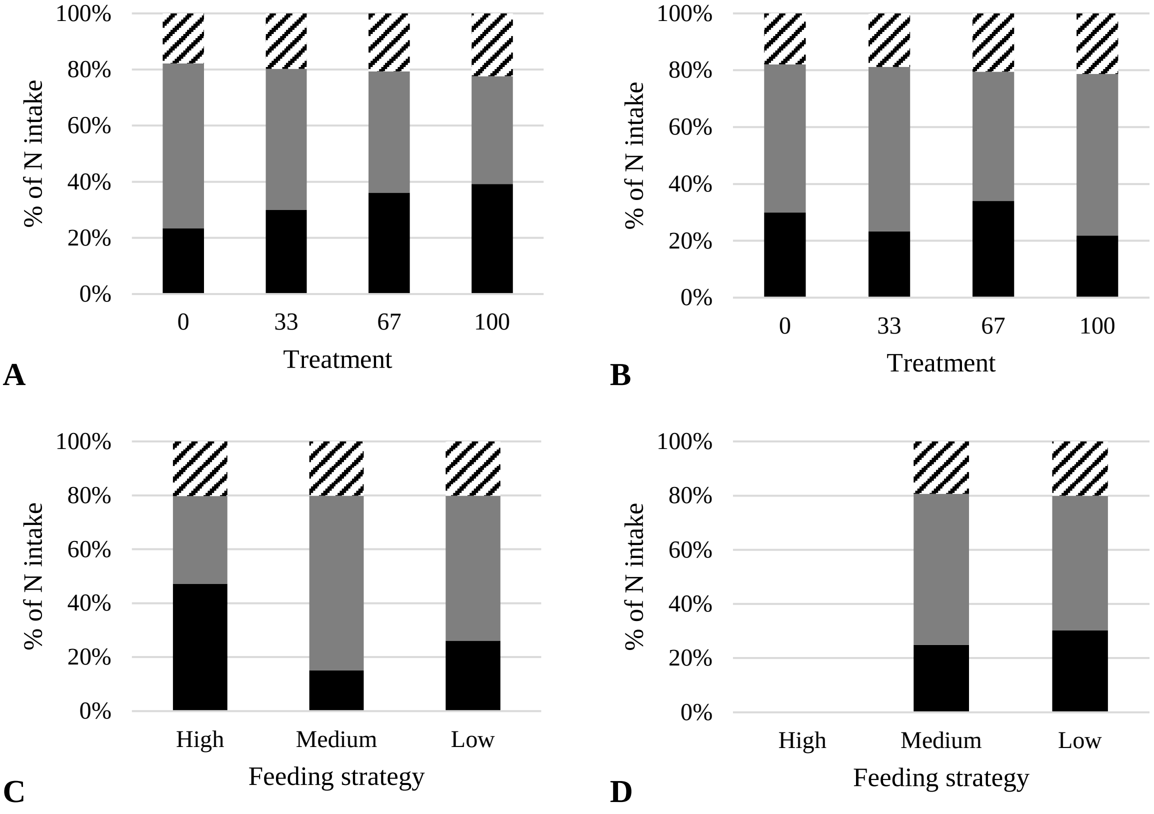

Figure legends:

Figure 1. Backfat (BF) thickness on days 0, 30, 60 and 108 after service, the feeding strategy groups, low (●), medium (■) and high (▲) are the groups defined at day 0, the limits defining the normal feeding strategy group at d 0 (12 to 16 mm BF) are represented by two dashed lines, whereas the target zone for all sows at day 108 (16 to 19 mm BF) is represented by two solid lines.

Figure 2. Fecal N output (striped), urine N output (gray) and N retention (black) as percentage of intake, in early (A) and mid (B) gestation, depending on treatment, with proportion of high-fiber diet (the rest is low-fiber diet) and depending on feeding strategy in early (C) and mid (D) gestation.

Table 1. Ingredients of the two experimental diets (as fed).

Item	Low fiber	High fiber
Ingredient, [g kg^{-1} as fed]		
Wheat	820	611
Barley	100	100
Sugar beet pulp	-	210
Soybean meal	27.8	34.1
Molasses	10	10
Leci E Basic[1]	5	5
Palm oil	5	5
Calcium carbonate	13.1	7.35
Sodium chloride	5.29	4.53
Monocalcium phosphate	5.06	5.08
L-Lys	1.93	1.31
L-Thr	0.6	0.52
Titaniumdioxide	3	3
Vitamin and mineral premix[2]	3.222	3.112

[1] Phospolipids, free fatty acid and triglycerides from rapeseed oil (Evilec Aps, Kolding, Denmark).

[2] Supplemented vitamins and minerals per kilogram of diet: 12000 IU retinol, 2000 IU 25-hydroxy vitamin D3 (Hy-D®, DSM Nutitional Products, Basel, Switzerland), 100 mg α-tocopherol, 5.00 mg phylloquinone, 2.0 mg thiamin, 0.04 mg cyanocobalamin, 8.00 mg riboflavin, 5.00 mg pyridoxine, 0.60 mg biotin, 25.0 mg D-pantothenic acid, 5.00 mg folic acid, 30.0 mg niacin, 85 mg Choline Extra (choline from a herbal source with no risk of chemical reactions with vitamins (AB Neo A/S, Videbæk, Denmark)), 86.0 mg iron ($FeSO_4$), 64.0 mg iron fumerate, 50.0 mg manganese (MnO), 50.0 mg zinc ($ZnSO_4$), 50.0 mg zinc chelated (Availa Zinc, Zinpro Corporation, Eden Praire, MN), 15.0 mg cupper as $CuSO_4$, 2.00 mg iodine ($Ca(IO_3)_2$), 0.25 mg selenium (Na_2SeO_3), 0.15 mg organic selenium (L-Selenomethionine, Excential Selenium 4000, Orffa, Breda, The Netherlands), 1500 FTU phytase (Ronozyme HiPhos GT, DSM Nutritional Products, Basel, Switzerland)

Table 2. Analyzed chemical composition (as fed) of experimental diets

Item[1]	0	33	67	100
Chemical composition,g×kg^{-1}				
DM	879	878	877	877
Ash	37.8	38.8	39.9	41.0
Fat	28.5	28.8	29.2	29.5
Starch	541	491	440	391
Soluble (S-NSP)	17.8	33.9	50.6	66.7
Insoluble non-starch polysacharides (I-NSP)	85.8	97.3	109.1	120.5
Klason-lignin	15.9	20.5	25.3	30.0
Dietary fiber	119	152	185	217
EDOM [2]	905	901	897	893
GE, MJ/kg	15.6	15.6	15.6	15.5
Energy, MJ ME/kg [3]	13.5	13.2	13.0	12.7
Energy, MJ net energy/kg [4]	10.3	10.0	9.8	9.6
Energy, Danish Feed Units/kg [5]	1.13	1.10	1.07	1.04
Titaniumdioxide	1.79	1.90	2.01	2.11
Protein and amino acids, g×kg^{-1} [6]				
CP	115 (86.0)	117 (87.7)	118 (89.4)	120 (91.1)
Lysine	5.47 (4.2)	5.34 (4.1)	5.21 (4.0)	5.09 (3.9)
Methionine	1.75 (1.3)	1.72 (1.3)	1.69 (1.3)	1.67 (1.3)
Threonine	4.16 (3.1)	4.25 (3.1)	4.33 (3.1)	4.42 (3.1)
Leucine	7.85 (6.1)	7.75 (6.1)	7.64 (6.1)	7.54 (6.1)
Valine	5.08 (3.8)	5.15 (3.8)	5.22 (3.9)	5.29 (3.9)
Minerals, g×kg^{-1}				
Sodium	1.85	1.88	1.90	1.93
Potassium	4.91	4.96	5.00	5.05
Magnesium	1.10	1.18	1.27	1.36
Calcium	7.04	6.94	6.85	6.76
Phosphorus	4.15	4.05	3.95	3.86
Trace minerals, mg×kg^{-1}				
Iron	281.3	296.2	311.6	326.5
Cupper	22.0	20.9	19.8	18.7
Manganese	66.8	69.5	72.2	74.9
Zinc	121.5	121.7	121.8	122.0

[1] Proportions of high-fiber diet, and rest refer to low fiber-diet.

[2] Enzyme digestible organic matter

[3] Calculated from Danish feed units (Theil et al., 2020)

[4] Calculated according to EvaPig (2008)

[5] Danish feeding units for sows: the Danish feed units are potential physiological energy, and this is closely related to net energy (Patience, 2012).

[6] Calculated standardized ileal digestibility values in brackets

Table 3. Apparent total tract digestibility of nutrients and energy in sows fed increasing levels of dietary fiber originating from sugar beet pulp with different feeding strategies in early (days 0 to 30) and mid (days 30 to 60) gestation[1]

	Dietary fiber (DF), g×kg^{-1} [2]											
	119	152	185	217		Feeding strategy (FS)[3]				*P*-value		
Item	0	33	67	100	SEM	High	Medium	Low	SEM	DF	FS	Linear
Early gestation												
n	**13**	**12**	**11**	**10**		**16**	**12**	**18**				
Dry matter (DM) digestibility, %	86.5^{a}	85.9^{a}	85.4^{bc}	85.0^{c}	0.28	85.6	85.9	85.6	0.27	<0.01	0.68	<0.001
Nitrogen (N) digestibility, %	82.2^{a}	80.7^{a}	79.2^{bc}	78.0^{c}	0.54	79.8	80.0	80.3	0.52	<0.001	0.77	<0.001
Non-starch polysaccharide (NSP) digestibility, %	64.3^{d}	70.2^{c}	75.6^{b}	79.5^{a}	0.85	71.1	73.5	72.7	0.82	<0.001	0.13	<0.001
Gross energy (GE) digestibility, %	86.7^{a}	85.9^{a}	85.1^{bc}	84.3^{c}	0.31	85.2	85.7	85.5	0.30	<0.001	0.59	<0.001
Organic matter digestibility, %	89.5^{a}	88.7^{b}	88.2^{bc}	87.7^{c}	0.22	88.4	88.7	88.6	0.22	<0.001	0.65	<0.001
Mid-gestation												
n[4]	**13**	**10**	**11**	**9**			**19**	**22**				
DM digestibility, %	86.2	86.5	85.7	85.7	0.50		86.3	85.7	0.35	0.54	0.20	0.24
N digestibility, %	82.2^{a}	81.4^{ab}	79.5^{ab}	79.0^{b}	0.88		80.9	80.2	0.61	<0.01	0.43	<0.001
NSP digestibility, %	63.3^{d}	71.1^{c}	75.6^{b}	80.8^{a}	0.87		73.5	71.9	0.60	<0.001	0.06	<0.001
GE digestibility, %	86.4	86.4	85.4	85.2	0.49		86.1	85.5	0.34	0.11	0.24	<0.05
Organic matter digestibility, %	89.2	89.2	88.5	88.4	0.39		89.0	88.6	0.27	0.20	0.27	0.05

[1] Data are least square mean values with their standard error of mean (SEM)

[2] Proportions of high-fiber diet, and rest refer to low-fiber diet.

[3] Feeding strategy at day 0 and 30: Backfat level: <12 mm: High, 12-16 mm: medium and >16 mm: Low

[4] Two sows were omitted (as compared with day 30) due to insufficient number of animals on the High FS

[a-d] Means within a row with different superscript differ ($P \leq 0.05$)

Table 4. Initial parameters, intake (as fed) and performance in early(days 0 to 30), mid(days 30 to 60) and late (days 60 to 108) gestation in sows fed increasing levels of dietary fiber originating from sugar beet pulp with different feeding strategies. [1].

	Dietary fiber (DF), g×kg^{-1} [2]											
	119	152	185	217		Feeding strategy (FS)[3]				*P*-value		
Item	0	33	67	100	SEM	High	Medium	Low	SEM	DF	FS	Linear
Initial parameters and sow performance												
n	13	12	11	10		16	12	18				
Parity	2.5	2.5	2.5	2.5	0	2.5	2.5	2.5	0	.	.	.
Sow bodyweight (BW) day 0, kg	231	224	234	227	8.22	214^{c}	224^{b}	248^{a}	7.90	0.83	<0.01	0.98
Sow backfat (BF) day 0, mm	14.0	13.9	14.7	14.5	0.58	11.1^{c}	14.1^{b}	17.6^{a}	0.56	0.72	<0.001	0.37
Body protein day 0[4], kg	37.2	35.3	36.7	35.3	1.36	34.9	35.0	38.5	1.23	0.54	<0.05	0.43
Body fat day 0[4], kg	57.1	58.9	62.0	57.2	4.16	49.7^{b}	56.4^{b}	70.3^{a}	3.76	0.73	<0.001	0.78
Total born piglets, n	19.8	18.7	21.7	23.1	1.60					0.20		0.06
Birth weight total litter, kg	24.3	24.8	25.6	26.1	1.60					0.82		0.35
Early gestation												
Average daily feed intake (ADFI), kg/d	2.83^{b}	2.88^{b}	2.96^{ab}	3.07^{a}	0.05	4.01^{a}	2.66^{b}	2.14^{c}	0.05	<0.01	<0.001	<0.001
Fiber intake, g/d	346^{d}	444^{c}	557^{b}	662^{a}	13.8	674^{a}	464^{b}	368^{c}	13.2	<0.001	<0.001	<0.001
BW gain, kg/d	0.417^{b}	0.478^{b}	0.705^{a}	0.596^{a}	0.065	0.957^{a}	0.491^{b}	0.199^{c}	0.062	<0.01	<0.001	<0.01
BF gain, mm/d	0.046	0.055	0.054	0.052	0.010	0.102^{a}	0.045^{b}	0.008^{c}	0.009	0.90	<0.001	0.68
Retained (body) protein (RP)[4], kg/d	0.061^{b}	0.072^{ab}	0.110^{a}	0.088^{ab}	0.014	0.129^{a}	0.081^{b}	0.038^{c}	0.013	<0.05	<.0001	<0.05
Retained (body) fat (RF)[4], kg/d	0.125	0.145	0.187	0.199	0.054	0.374^{a}	0.110^{b}	0.008^{b}	0.049	0.63	<0.001	0.21
BW gain:feed ratio, kg/kg$_{feed}$	0.139^{b}	0.146^{b}	0.238^{a}	0.190^{ab}	0.025	0.266^{a}	0.179^{b}	0.089^{c}	0.024	<0.05	<0.001	<0.05
BF gain:feed ratio, mm/kg$_{feed}$	0.014	0.016	0.017	0.016	0.004	0.028^{a}	0.016^{b}	0.003^{c}	0.004	0.96	<0.001	0.66
RP:feed ratio[4], kg/kg$_{feed}$	0.021^{b}	0.023^{ab}	0.038^{a}	0.029^{ab}	0.006	0.036^{a}	0.030^{ab}	0.017^{b}	0.005	<0.05	<0.01	0.06

RF:feed ratio^{4}, kg/kg$_{\text{feed}}$	0.038	0.045	0.057	0.061	0.021	0.104^{a}	0.041^{b}	0.006^{b}	0.019	0.80	<0.001	0.34
Retained protein energy (RPE) ^{5}, % of ME$_{\text{Intake}}$	3.7^{b}	4.7^{ab}	7.2^{a}	4.8^{ab}	1.1	6.4	5.5	3.4	1.0	<0.05	<0.05	0.14
Retained fat energy RFE^{5}, % of ME$_{\text{Intake}}$	10	15	17	20	7.7	31^{a}	13^{b}	2^{b}	7.2	0.75	<0.01	0.30
Retained energy RE^{5}, % of ME$_{\text{Intake}}$	14	20	25	25	7.5	38^{a}	18^{b}	6^{b}	7.1	0.56	<0.01	0.21
Mid-gestation												
n^{6}	12	10	11	8			19	22				
ADFI, kg/d	2.12	2.13	2.15	2.18	0.05		2.36^{a}	1.93^{b}	0.032	0.78	<0.001	0.31
Fiber intake, g/d	253^{d}	329^{c}	407^{b}	476^{a}	8.3		402^{a}	331^{b}	17.9	<0.001	<0.001	<0.001
BW gain, kg/d	0.37	0.49	0.36	0.45	0.082		0.49	0.34	0.057	0.53	0.08	0.81
BF gain, mm/d	0.016	0.023	0.003	0.023	0.012		0.032	0.000	0.007	0.35	<0.01	0.96
RP^{4}, kg/d	0.042	0.060	0.055	0.060	0.017		0.068	0.041	0.012	0.79	0.11	0.45
RF^{4}, kg/d	0.23	0.28	0.20	0.19	0.058		0.30	0.14	0.039	0.58	<0.01	0.40
BW gain:feed ratio, kg/kg$_{\text{feed}}$	0.18	0.23	0.16	0.21	0.038		0.21	0.18	0.026	0.50	0.36	0.85
BF gain:feed ratio, mm/kg$_{\text{feed}}$	0.020	0.027	0.025	0.029	0.008		0.029	0.022	0.005	0.84	0.36	0.45
RP:feed ratio^{4}, kg/kg$_{\text{feed}}$	0.007	0.009	0.000	0.011	0.005		0.014	0.000	0.003	0.35	<0.01	1.00
RF:feed ratio^{4}, kg/kg$_{\text{feed}}$	0.108	0.137	0.090	0.091	0.029		0.138	0.075	0.019	0.50	<0.05	0.40
RPE^{5}, % of ME$_{\text{Intake}}$	3.7	5.2	4.7	5.4	1.5		5.4	4.1	1.0	0.79	0.37	0.45
RFE^{5}, % of ME$_{\text{Intake}}$	33	42	27	28	9.0		42^{a}	23^{b}	6.0	0.56	<0.05	0.42
RE^{5}, % of ME$_{\text{Intake}}$	37	47	32	33	9.0		48^{a}	27^{b}	6.0	0.55	<0.05	0.49
Late gestation)												
n	12	10	11	10								
ADFI, kg/d	2.65^{c}	2.67^{c}	2.75^{b}	2.83^{a}	0.02					<0.001		<0.001

Fiber intake, g/d	306^d	390^c	479^b	590^a	4	<0.001	<0.001
BW gain, kg/d	0.70	0.64	0.58	0.70	0.06	0.39	0.74
BF gain, mm/d	0.016	0.016	0.008	0.009	0.008	0.81	0.39
RP[4], kg/d	0.032	0.046	0.036	0.060	0.013	0.42	0.21
RF[4], kg/d	0.17	0.11	0.03	0.12	0.074	0.46	0.39
BW gain:feed ratio ($\text{kg/kg}_{\text{feed}}$)	0.26	0.24	0.21	0.25	0.021	0.32	0.34
BF gain:feed ratio ($\text{mm/kg}_{\text{feed}}$)	0.012	0.017	0.013	0.021	0.005	0.51	0.29
RP:feed ratio[4], $\text{kg/kg}_{\text{feed}}$	0.006	0.006	0.003	0.003	0.003	0.78	0.34
RF:feed ratio[4], $\text{kg/kg}_{\text{feed}}$	0.066	0.040	0.010	0.041	0.027	0.44	0.33

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[1] Data are least square mean values with their standard error of mean (SEM)

[2] Proportion of high-fiber diet, and rest refer to low-fiber diet.

[3] Feeding strategy at day 0 and 30: Backfat level: <12 mm: High, 12-16 mm: medium and >16 mm: Low

[4] Retained protein and fat, calculated from the deuterium oxide (D_2O) dilution technique

[5] Retained energy as protein: Retained protein × 23.9 MJ/kg and retained energy as fat: retained fat × 39.8 MJ/kg as percentage of experimental found metabolizable energy (ME) intake (Table 6).

[6] Two sows were omitted (as compared with day 0 to 30) due to insufficient number of animals on the High FS

[a-d] Means within a row with different superscript differ ($P \leq 0.05$)

Table 5. Plasma metabolites in sows fed increasing levels of dietary fiber originating from sugar beet pulp with different feeding strategies in early (day 30) and mid (day 60) gestation[1]

	Dietary fiber (DF), g×kg^{-1} [2]											
	119	152	185	217		Feeding strategy (FS)[3]				*P*-value		
Item	0	33	67	100	SEM	High	Medium	Low	SEM	DF	FS	Linear
Gestation day 30												
n	**13**	**12**	**11**	**10**		**16**	**12**	**18**				
Nonesterified fatty acid (NEFA), µekv./L	44.6	45.4	66.7	53.5	8.5	36.0^{b}	52.8^{ab}	68.8^{a}	7.8	0.16	<0.01	0.14
Glucose, mmol/L	4.22	4.42	4.57	4.24	0.14	4.52	4.25	4.31	0.13	0.20	0.33	0.61
Urea, mmol/L	3.17	3.00	2.81	2.79	0.13	3.52^{a}	2.85^{b}	2.46^{c}	0.13	0.11	<0.001	<0.05
Lactate, mmol/L	2.05^{b}	3.28^{a}	1.48^{b}	1.54^{b}	0.40	2.17	2.13	1.96	0.38	<0.01	0.88	0.05
Triglyceride, mmol/L	0.34^{b}	0.44^{a}	0.42^{a}	0.35^{b}	0.02	0.41	0.39	0.36	0.02	<0.01	0.21	0.72
Gestation day 60												
n[4]	**13**	**10**	**11**	**9**			**19**	**22**				
NEFA, µekv./L	58.0	58.7	52.2	60.0	10.6		44.8^{b}	79.4^{a}	7.05	0.77	<0.01	0.34
Glucose, mmol/L	4.54	4.48	4.62	4.55	0.12		4.42	4.57	0.08	0.94	0.20	0.64
Urea, mmol/L	2.68^{a}	2.44^{ab}	2.40^{ab}	2.19^{b}	0.11		2.49	2.37	0.08	<0.05	0.28	<0.01
Lactate, mmol/L	1.89	1.58	1.22	1.71	0.26		1.64	1.56	0.19	0.20	0.74	0.33
Triglyceride, mmol/L	0.39	0.42	0.42	0.39	0.03		0.40	0.41	0.02	0.75	0.66	0.87

[1] Data are least square mean values with their standard error of mean (SEM)

[2] Proportions of high-fiber diet, and rest refer to low-fiber diet.

[3] Feeding strategy at day 0 and 30: Backfat level: <12 mm: High, 12-16 mm: medium and >16 mm: Low

[4] Two sows were omitted (as compared with day 30) due to insufficient number of animals on the High FS

[a-c] Means within a row with different superscript differ ($P \leq 0.05$)

Table 6. Realized nitrogen (N) and gross energy (GE) intake, output and total retention (RE) in sows fed increasing levels of dietary fiber originating from sugar beet pulp with different feeding strategies in early (days 0 to 30) and mid (days 30 to 60) gestation[1]

	Dietary fiber (DF), g×kg^{-1} [2]											
	119	152	185	217		Feeding strategy (FS)[3]				*P*-value		
Item	0	33	67	100	SEM	High	Medium	Low	SEM	DF	FS	Linear
Early gestation												
n	13	12	11	10		16	12	18				
Realized N intake, g/d	52.2^{c}	53.9^{bc}	56.2^{b}	58.9^{a}	0.9	75.4^{a}	50.3^{b}	40.3^{c}	0.9	<0.001	<0.001	<0.001
Urine N output, g/d	30.6	26.9	24.3	22.6	4.3	24.6	32.4	21.3	4.2	0.51	0.12	0.14
Fecal N output, g/d	9.3^{c}	10.5^{bc}	11.6^{b}	13.1^{a}	0.45	15.3	10.1	8.0^{c}	0.31	<0.001	<0.001	<0.001
Total N retention[4], g/d	12.2	16.0	20.3	23.0	3.9	35.7^{a}	7.6^{b}	10.3^{b}	3.8	0.18	<0.001	<0.05
Heart rate, average, bpm.	96.8	87.3	93.5	90.8	5.3	95.4	91.4	89.6	5.1	0.57	0.66	0.58
GE intake, MJ/d	44.2^{b}	44.9^{b}	46.1^{ab}	47.8^{a}	0.76	62.5^{a}	41.5^{b}	33.3^{c}	0.78	<0.01	<0.001	<0.001
Urine GE output[5], MJ/d	1.5	1.4	1.2	1.1	0.22	1.2	1.6	1.1	0.21	0.51	0.12	0.14
Fecal GE output, MJ/d	5.9^{c}	6.4^{b}	6.9^{a}	7.5^{a}	0.18	9.2^{a}	6.0^{b}	4.8^{c}	0.17	<0.001	<0.001	<0.001
Methane GE output[6], MJ/d	0.2^{d}	0.3^{c}	0.4^{b}	0.5^{a}	0.01	0.5^{a}	0.3^{b}	0.3^{c}	0.0	<0.001	<0.001	<0.001
ME[7], MJ/d	36.5^{b}	36.6^{b}	37.7^{a}	38.5^{a}	0.57	51.8^{a}	33.5^{b}	26.6^{c}	0.64	<0.05	<0.001	<0.01
Heat energy total[8], MJ ME/d	28.9	25.8	27.8	26.9	1.7	28.4	27.1	26.5	1.6	0.57	0.66	0.58
RE$_{GE}$[9], MJ/d	7.9	8.8	9.7	11.5	2.2	23.9^{a}	5.4^{b}	-0.8^{c}	1.99	0.61	<0.001	0.19
Realized dietary ME[10], MJ/kg	12.9	12.8	12.7	12.6	0.08	12.9^{a}	12.6^{b}	12.7^{ab}	0.08	0.13	<0.05	<0.05
Mid-gestation												
n [11]	12	10	11	8			19	22				
Realized N intake, g/d	39.0	39.7	40.8	41.8	0.87		44.4^{a}	36.3^{b}	0.60	0.08	<0.001	<0.05

Urine N output, g/d	20.4	23.0	18.5	23.8	3.1	24.7^{a}	18.1^{b}	2.2	0.53	<0.05	0.69
Fecal N output, g/d	7.0^{b}	7.5^{bc}	8.4^{ab}	8.9^{a}	0.45	8.6^{a}	7.3^{b}	0.31	<0.01	<0.01	<0.001
Total N retention[4], g/d	11.7	9.3	13.9	9.1	2.8	11.0	11.0	1.9	0.50	0.98	0.84
Heart rate, average, bpm.	100.0	92.5	90.9	85.3	5.7	96.8	87.5	11.9	0.26	0.11	0.06
GE intake, MJ/d	33.1	33.1	33.5	33.9	0.72	36.7^{a}	30.1^{b}	0.50	0.85	<0.001	0.39
Urine GE output[5], MJ/d	1.0	1.2	0.9	1.2	0.16	1.2^{a}	0.9^{b}	0.11	0.53	<0.05	0.69
Fecal GE output, MJ/d	4.5	4.6	4.9	5.1	0.21	5.2^{a}	4.4^{b}	0.14	0.13	<0.001	<0.05
Methane GE output[6], MJ/d	0.2^{d}	0.2^{c}	0.3^{b}	0.4^{a}	0.0	0.3^{a}	0.2^{b}	0.0	<0.001	<0.001	<0.001
ME[7], MJ/d	27.4	27.2	27.4	27.3	0.56	30.1^{a}	24.6^{b}	0.39	0.99	<0.001	0.91
HE total[8], MJ ME/d	29.9	27.5	27.0	25.2	1.8	28.9	25.9	1.3	0.25	0.11	0.06
RE$_{GE}$[9], MJ/d	-2.5	-0.4	0.4	2.1	1.91	4.5	1.5	1.4	0.31	0.19	0.07
Realized dietary ME[10], MJ/kg	12.9	12.9	12.7	12.6	0.11	14.2	14.3	0.14	0.09	0.81	<0.05

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[1] Data are least square mean values with their standard error of mean (SEM)

[2] Proportion of high-fiber diet, and rest refer to low-fiber diet.

[3] Feeding strategy at day 0 and 30: Backfat level: <12 mm: High, 12-16 mm: medium and >16 mm: Low

[4] N intake - (Urine N output + Fecal N Output)

[5] Assuming that energy in urine from sows contains 50.4 kJ/g N (Theil et al., 2002a, 2004)

[6] 0.0628+0.00488×Fermented fiber, g/kg dry matter (Jørgensen et al., 2011)

[7] GE intake - (Urine GE output + Methane GE output + Feces GE output)

[8] Calculated using the heart rate and heat energy (HE) relationship (Krogh et al., 2018)

[9] ME intake - HE total

[10] (GE intake - (Urine GE output + Methane GE output + Fecal GE output))/average daily feed intake

[11] Two sows were omitted (as compared with day 30) due to insufficient number of animals on the High FS

[a-d] Means within a row with different superscript differ ($P \leq 0.05$)

5.5. Paper II

Influence of four fiber-rich supplements on digestibility of energy and nutrients and utilization of energy and nitrogen in early and mid-gestating sows.

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Non ruminant nutrition

Influence of four fiber-rich supplements on digestibility of energy and nutrients and utilization of energy and nitrogen in early and mid-gestating sows

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Abstract

The digestibility of energy and nutrients in fiber-rich diets depends greatly on the fiber source but most data are from studies with growing pigs. The purpose of this study was to investigate the apparent total tract digestibility (**ATTD**) of nutrients in different fiber-rich diets and to quantify whole-body metabolism and utilization of energy and nitrogen (**N**) in gestating sows. Four fiber-rich diets based on sugar beet pulp (**SBP**), soy hulls (**SH**), palm kernel expellers (**PKE**), or a mixed fiber (**MF**) were formulated, with an average daily intake of total fiber (**TF**) of 471, 507, 651, and 437 g/d, respectively. A total of 48 multiparous sows were stratified by body weight at mating (day 0) and assigned to one of the four diets throughout gestation. Body weight and backfat were measured, and body pools of fat and protein were estimated using the deuterium oxide dilution technique at days 0, 30, and 60. On days 30 and 60, urine and fecal grab samples were obtained. On days 15 and 45, heart rate was measured to estimate total heat production. The ATTD of nutrients differed across treatments ($P < 0.001$), while in vivo organic matter digestibility deviated with up to ±3.3% units from in vitro enzyme digestibility of organic matter. The ATTD of energy was highly negatively correlated with intake of lignin ($P < 0.001$), while ATTD of N was highest (negatively) correlated ($P < 0.001$) with intake of insoluble non-starch polysaccharides (**NSP**). The ATTD of all nutrients except NSP was lowest in PKE-fed sows and highest, except for N, in sows fed the SBP diet. The ATTD of N was highest in the MF-fed sows and ATTD of NSP was lowest in the MF-fed sows. Sows lost most energy as heat (53% to 72% of gross energy intake), followed by energy in feces (15% to 17%), urine (3% to 4%), and methane (0.5% to 0.9%). Energy for maintenance accounted for the majority of the heat production and the total energy retention was lowest and highest in the SBP- and PKE-fed sows, with a retention of 3.3 and 13.3 MJ/d, respectively ($P < 0.001$). Sows lost most N through urine, the lowest and highest N loss (relative to intake) was observed in SH- and SBP-fed sows (50% to 63%, respectively), while 14% to 26% was retained as body protein. In conclusion, the fiber-rich diets were utilized efficiently by gestating sows with respect to energy with ATTD values above 82% in all four fiber-rich diets, whereas the high TF content in the diets compromised the N utilization in gestating sows.

Lay Summary

How much energy and nutrients a pig can use from the feed depends greatly on the feed ingredients, feed level, and the physiological stage of the animal. Fibers are of great interest because they can improve health and welfare of pigs and co-products from the food and agriculture industries are among the most interesting. The ability to degrade different fiber sources and utilize energy and nutrients are poorly understood in gestating sows, but highly important when formulating the feed composition. The hypothesis was that sugar beet pulp was superior to the other three fiber-rich sources investigated: soy hulls, palm kernel expellers, or a mix of fibers, with respect to intake and utilization of energy and nutrients. We did not find sugar beet pulp to be particularly superior with respect to energy (fermentation or utilization), whereas utilization of nitrogen was highest for sugar beet pulp but compromised in the three other diets depending on fiber sources.

Key words: feed efficiency, heat production, protein quality, sow nutrition, total fiber

Abbreviations: ADFI, average daily feed intake; ATTD, apparent total tract digestibility; BF, backfat; BW, body weight; CP, crude protein; D_2O, deuterium oxide; DM, dry matter; GE, gross energy; HP, heat production; I-NCP, insoluble non-cellulosic polysaccharides; I-NSP, insoluble non-starch polysaccharide; ME, metabolizable energy; MF, mixed fiber; N, nitrogen; NE, net energy; NEFA, non-esterified fatty acid; NSP, non-starch polysaccharide; OM, organic matter; PKE, palm kernel expellers; SBP, sugar beet pulp; SCFA, short-chain fatty acid; SH, soy hulls; S-NSP, soluble non-starch polysaccharides; TAG, triglycerides; TF, total fiber; TiO_2, titanium dioxide

Introduction

The interest in feeding high-fiber diets to gestating sows is increasing because of economical, animal health, and welfare perspectives (Le Goff et al., 2002), but the nutritional values (energy and protein) of fiber-rich feedstuffs are poorly studied in sows (Slama et al., 2019). Increasing the total fiber (**TF**) defined as non-starch polysaccharides (**NSP**) and lignin (Bach Knudsen and Lærke, 2018), concentration decreases the energy digestibility and thereby metabolizable and net energy in diets (Theil et al., 2020). Since the organic matter (**OM**) digestibility is the main factor determining the energy value of the feed, it is important to know the OM

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digestibility of fiber-rich materials (Beecher et al., 2015). It is widely known that the digestibility of nutrients depends on age and physiological state of the animal, and this is especially pronounced for the fermentation of fibers (Noblet and Shi, 1993; Jacyno et al., 2016) because sows have a higher fermentative capacity than growing pigs (Che et al., 2011; Li et al., 2019) caused by a longer retention time in the large intestine (Jha and Berrocoso, 2015). The fermentation of fiber also depends on the type and composition of fiber, that is, the proportion of soluble and insoluble fiber, as well as the lignification of the fiber fraction. In general, soluble fibers are more fermentable than insoluble fibers (Noblet and Le Goff, 2001; Renteria-Flores et al., 2008), and a higher degree of lignification generally decreases fiber degradation (Noblet and Le Goff, 2001).

Sows are able to utilize the metabolites from fiber fermentation for fat retention almost as efficiently as dietary starch in early gestation (Wisbech et al., 2022), and fiber inclusion level may be doubled (35% to 40% of feed DM) without affecting the feeding motivation (Jensen et al., 2012). Soluble fiber may also improve satiety and attenuate physical activity (Rijnen et al., 2003; Holt et al., 2006; Jørgensen et al., 2010) and improve the health of the gastrointestinal tract (Zhuo et al., 2020; Grześkowiak et al., 2022). Nutritionally, fibers may affect the digestibility of protein and the absorption kinetics of various nutrients important for animal performance, and in turn affect the excretion of nutrients and the environmental impact.

The aim of this study was to investigate how the fibers affect the total tract digestibility of nutrients, and how they influence whole-body metabolism and utilization of energy and nitrogen (**N**). Four fiber-rich diets provided with either sugar beet pulp (**SBP**), soy hulls (**SH**), palm kernel expellers (**PKE**), or a mixed fiber (**MF**; sugar beet pulp, oat hulls, wood fibers, and yeast) were formulated and fed to gestating sows. It was hypothesized that the energy and N digestibility, utilization, and retention were superior in sows fed SBP, due to the combination of high soluble fiber and low lignin content, as compared with other fiber sources studied.

Materials and Methods

The animal experimental procedures and care of animal under study were carried out in accordance with the Ministry of Food, Agriculture and Fisheries, The Danish Veterinary and Food Administration under act 474 of 15 May 2014 and executive order 2028 of 14 December 2020. A license was obtained from the Danish Animal Experiments Inspectorate. The trial was carried out at Aarhus University, Foulum.

Experimental design, animals, and housing

The experiment consisted of two blocks with each two periods: early gestation from days 0 to 30 of gestation and mid-gestation from days 30 to 60. Forty-eight (12 per treatment) multiparous (3rd and 4th parity) crossbreed sows (DanBred Landrace × DanBred Yorkshire) were stratified according to bodyweight at weaning and backfat thickness and allocated to one of the four dietary treatments. Sows were individually housed in crates (65 × 245 cm) with partly slatted floors in the two periods. The light was turned on for 18 h each day and the temperature was kept constant at 18 °C.

Dietary treatments and feeding

The experimental diets were composed of a basal component containing mainly wheat (80.5%), barley (10%), and soybean meal (3.7%) and one of the four fiber-rich supplements were then added. The supplements primarily consisted of either SBP, SH, PKE, or MF, the latter being a mix of SBP, oat hulls, OptiCell (natural fiber from wood; Agromed GmbH, Kremsmünster, Austria), Progress (containing free fatty acids and resin acid; Hankkija Oy, Hyvinkää/Suomen Rehu, Finland), and Progut (hydrolyzed yeast product containing both cell wall and extracted parts, hence rich in betaglucans, mannoproteins, nucleotides, and peptides; Hankkija Oy/Suomen Rehu, Hyvinkää, Finland). Titanium dioxide (**TiO_2**) was added to the basal component as an indigestible marker to quantify the digestibility of nutrients (Table 1). The experimental diets consisted of 2.22 and 1.78 kg of the basal component in early and mid-gestation periods, respectively, and then an additional 0.43 kg SBP, 0.41 kg SH, 0.71 kg PKE, or 0.51 kg MF (as an average across the two periods), based on tabulated values for SBP, SH and partly MF from the commonly used Danish database for feedstuffs (SEGES, 2019a) and PKE from Bach Knudsen (1997), to achieve equal amounts of TF fed daily. The experimental diets complied with the nutrient requirements for gestating sows (Tybirk et al., 2020) and diet formulation and daily allowance was calculated in the Danish feed unit for sows, which is closely related to net energy (Patience, 2012). The animals were supplied feed slightly above maintenance in early gestation and at maintenance level in mid-gestation as recommended for sows with normal body conditions in Denmark (SEGES, 2019b).

Both the basal component and the supplements were produced by Vestjyllands Andel (Ringkøbing, Denmark) and delivered as pellets at the experimental facility, and the basal component and supplements were mixed before each meal. The sows were fed twice daily (0900 and 1400 hours), and feed leftover, if any, were collected to determine their realized feed intake. However, the pellet quality of the PKE supplement was poor and therefore more PKE supplement was wasted from the feed trough, resulting in a risk for underestimating feed leftover. Representative samples from the basal component and fiber-rich supplements were collected every third week and stored at −20 °C prior to pooling. At the end of the experiment, pooled samples were then analyzed for chemical composition.

Sampling and data collection

At mating (day 0), body weight (**BW**) and backfat (**BF**) were recorded and body pools of protein and fat were estimated using the deuterium oxide (**D_2O**) technique (Rozeboom et al., 1994). On days 30 and 60 of gestation, urine, feces, and blood samples were collected. On days 15 and 45, heart rate was measured and at farrowing, litter size (total born) and litter weight was recorded.

Backfat scanning was done at the P2 position; at the last rib, 6 cm down from the spine. To ensure measurements were done at the same position at subsequent recordings, a dot was tattooed at both the left and right P2 positions of the sow. Three consecutive scans were performed at each side using a Lean-Meater (Renco Corp., Minneapolis, MN, USA) and the mean value of the six scans was used as the mean BF.

Prior to D_2O enrichment of the sows, a urine sample was collected to determine the background contribution of D_2O.

Table 1. Ingredients of the basal component and the fiber-rich supplements (as fed)

		Fiber-rich supplements			
Item	**Basal component**	**Sugar beet pulp**	**Soy hulls**	**Palm kernel expellers**	**Mixed fiber**
Ingredient, % as fed					
Wheat	80.45				
Barley	10.00				
Soybean meal, dehulled	3.70				
Calcium carbonate	1.56				
Leci E Basic[1]	1.00	2.00	2.00	2.00	2.00
Sugar beet molasses	1.00	1.00	1.00	1.00	1.00
Monocalcium phosphate	0.84				
Sodium chloride	0.65				
L-Lysine HCL (98.5%)	0.26				
L-Threonine	0.10				
DL-Methionine	0.01				
Sugar beet pulp, pelleted		96.92			51.92
Oat hulls					30.00
Opticell[2]					12.50
Progress[3]					1.50
Progut[4]					1.00
Palm kernel expellers				96.92	
Soy hulls			96.92		
Premix	0.09[5]	0.08[6]	0.08[6]	0.08[6]	0.08[6]
Titanium dioxide	0.35				

[1] Phospolipids, free fatty acid, and triglycerides derived from rapeseed oil (Evilec Aps, Kolding, Denmark).

[2] An insoluble partly fermentable dietary fiber source derived from three tree species (Agromed Austria GmbH, Kremsmünster, Austria).

[3] A resin acid-based product derived from trees containing ~0.8% resin acid, ~90% free fatty acids, and 2% to 3% natural occurring components in trees (Hankkija Oy/Suomen Rehu, Hyvinkää, Finland).

[4] Hydrolyzed yeast cell walls and extracts which contain betaglucans, mannoproteins, nucleotides, and peptides (Hankkija Oy/Suomen Rehu, Hyvinkää, Finland).

[5] Supplemented vitamins and minerals per kg of diet: 9,020 IU retinol, 50 µg 25-hydroxy vitamin D3 (Hy-D, DSM Nutitional Products, Basel, Switzerland), 101 mg α-tocopherol, 4.51 mg menadion, 2.25 mg thiamin, 0.02 mg cyanocobalamin, 5.63 mg riboflavin, 3.38 mg pyridoxine, 0.45 mg biotin, 16.9 mg D-pantothenic acid, 1.69 mg folic acid, 22.5 mg niacin, 90.2 mg iron ($FeSO_4$), 45.1 mg manganese (MnO), 112.70 mg zinc sulfate ($ZnSO_4$), 13.0 mg copper as $CuSO_4$, 0.23 mg iodine ($Ca(IO_3)_2$), 0.39 mg selenium as sodium selenite (Na_2SeO_3), 1,500 FTU phytase (Ronozyme HiPhos GT, DSM Nutritional Products, Basel, Switzerland).

[6] Supplemented vitamins and minerals per kg of diet: 8,000 IU retinol, 50 µg 25-hydroxy vitamin D3 (Hy-D, DSM Nutitional Products, Basel, Switzerland), 90.0 mg α-tocopherol, 4.00 mg menadion, 2.00 mg thiamin, 0.02 mg cyanocobalamin, 5.00 mg riboflavin, 3.00 mg pyridoxine, 0.40 mg biotin, 15.0 mg D-pantothenic acid, 1.50 mg folic acid, 20.0 mg niacin, 80.0 mg iron ($FeSO_4$), 40.0 mg manganese (MnO), 100.0 mg zinc sulfate ($ZnSO_4$), 13.0 mg copper as $CuSO_4$, 0.20 mg iodine ($Ca(IO_3)_2$), 0.35 mg sodium selenite (Na_2SeO_3).

The sows were then enriched when receiving their morning feed through intramuscular injection of 0.0425 g/kg BW using a 40% D_2O solution, which was prepared by diluting 99.9% D_2O (Sigma-Aldrich, St. Louis, MO, USA) with saline. About 4 h after enrichment, a 4 mL blood sample was collected in heparinized vacutainer tubes (Greiner Bio-One, GmbH, Kremsmünster, Austria) from the jugular vein. Furthermore, on days 30 and 60 of gestation, a 9 mL blood sample was collected 4 h (range 3 to 5 h) after feeding. Samples were stored on ice until centrifugation for 10 min at 1,558 × *g* at 4 °C and plasma was harvested and stored at −20 °C until analysis.

A urinary balloon catheter size 20 (Teleflex Medical, Kamunting, Malaysia) was inserted and the urinary bladder was emptied before a stopper was placed to ensure urine stayed in the bladder. The bladder was then emptied every second hour, and the total amount of urine was collected for approximately 6 h during the day. Urine was collected in a 10 L container which was closed immediately after transfer from the bladder and kept cold until the end of the collection period. The amount of urine was recorded, pH was measured using a portable pH meter (B-71x LAQUAtwin, Horiba Scientific, NJ, USA), and a pooled subsample was stored at −20 °C for further analysis. A fresh fecal sample was also collected on the same sampling day and stored at −20 °C for later analysis. Heart rate was measured using a tracker (Polar Team Pro GPS tracking system, Polar, Ballerup, Denmark), which was mounted on an elastic belt, fitted just behind the front legs around the chest of the sow. The heart rate measurements were initiated when all sows had completed their morning meal and lasted four to five hours.

Chemical analysis

Both samples of the basal component and the four fiber-rich supplements were analyzed for dry matter (**DM**) by drying the sample for 20 h at 103 °C in a forced air oven. Gross energy (**GE**) was determined in an Automatic Isoperibol Calorimetry system (Parr Instrument Company, Moline, Illinois, USA). Ash, N, amino acids, crude fat, vitamins, and minerals were analyzed according to the Official Journal of the European Union (EU; 152/2009). Starch, NSP divided in soluble NSP (**S-NSP**), insoluble NSP (**I-NSP**) as cellulose, and insoluble non-cellulosic polysaccharides (**I-NCP**) and Klason lignin were analyzed according to Bach Knudsen (1997). In the basal component, TiO2 was analyzed in duplicate as described by Short et al. (1996), and the TiO_2 concentrations in the four diets were calculated based on the proportional intake of DM from basal component and fiber-rich supplements.

The fecal samples were analyzed for DM, GE, starch, NSP, Klason lignin, and TiO_2 as described for feed except that TiO_2 was not analyzed in duplicate. Nitrogen was analyzed using the Dumas method (Hansen, 1989) on a Vario Max CN Element analyzer (Elementar Analysensytem GmbH, Langenselbold, Germany) using aspartic acid as a calibrating standard. Urine N was analyzed using the Kjeldahl method (method 984.13; AOAC Int., 2000) on a KjelTecTM 2400 (Foss, Hillerød, Denmark). To determine the D_2O space, the atomic fraction was measured in urine (representing background enrichment) and plasma (representing D_2O enrichment after equilibration), and this was done after ultrafiltration of urine or plasma according to the method described by Theil et al. (2002b). The concentration of non-esterified fatty acids (**NEFA**) in plasma was determined using the Wako, NEFA C ACS-ACOD method (Wako Chemicals GmbH, Neuss, Germany), while the plasma concentrations of glucose, urea, lactate, and triglycerides were measured using the standard assays from Siemens Diagnostics (Siemens Diagnostics Clinical Methods for ADVIA 1650) using an auto-analyzer (ADVIA 1650 Chemistry System, Siemens Medical Solution, Tarrytown, NY, USA).

Calculations and statistical analysis

Crude protein (**CP**) was calculated as N × 6.25 in diets and feces. The apparent total tract digestibility (**ATTD**) of nutrients and energy were calculated using TiO_2 as a marker, (with N as an example):

$$ATTD\ N\ \ [\%] = 100 - \left(100\ \times \frac{Diet\ TiO\ \ [\%]}{Fecal\ TiO\ \ [\%]} \times \frac{Fecal\ N\ \ [\%]}{Diet\ N\ \ [\%]}\right)$$

The daily N loss in urine was calculated by multiplying the total N loss by 1,440 and dividing it with the collection time (approx. 6 h) in minutes. For energetic calculations, it was assumed that urine contains 50.41 kJ/g of N (Theil et al., 2002a, 2004). The heat production (HP) was calculated using the average heart rate, according to Krogh et al. (2018):

$$\mathrm{HE}\quad (\mathrm{MJ/d}) = 0.323\left(\frac{\mathrm{MJ}}{\mathrm{d}}/\mathrm{bpm}\right)$$
$$\times \mathrm{average}\quad \mathrm{heart}\quad \mathrm{rate}\quad (\mathrm{bpm}) - 2.4\quad (\mathrm{MJ/d})\,.$$

Retained protein and fat using the D_2O dilution technique and whole body N and energy balances in the sow were calculated as described by Wisbech et al. (2022).

The mixed model in the SAS software (version 9.4, SAS Institute Inc., Cary, NC, USA, 2012) was used to apply the following model:

$$Y_{ijk} = \mu + \alpha_i + \beta_j + \tau_k + \varepsilon_{ijk},$$

where Y_{ijk} is the response variable, μ is the overall mean, α_i is the fixed effect of treatment (SBP, SH, PKE, and MF), β_j is the fixed effect of period (early, mid), τ_k is the random effect of block (1 and 2), and ε_{ijk} is the residual error component, which was assumed to be normally distributed $N\left(0, \sigma^2\right)$. The results are presented as means ± standard error of means (**SEM**), where the highest SEM for treatment and period, respectively, are shown. The interaction between treatment and period was tested, but not found significant for any traits and hence excluded from the final model. The CORR procedure in SAS was used to determine the correlations. A probability value of $P \le 0.05$ was considered significant, and as a tendency when $0.05 < P \le 0.10$.

Results

Total fiber concentration was 114 g/kg (as-is) in the basal component and it ranged from 411 to 650 g/kg in the fiber-rich supplements (Table 2). In the experimental diets, the TF concentration ranged from 176 (MF diet) to 243 (PKE diet) g/kg. The S-NSP accounted for 15%, 19%, 24%, and 30% and lignin for 17%, 10%, 16%, and 13% of total TF in PKE, SH, MF, and SBP diets, respectively. The GE content was highest in the PKE diet (18.2 MJ/kg) followed by MF, SH, and SBP (17.7, 17.5, and 17.4 MJ/kg), respectively.

Average daily intake of energy and nutrients and digestibility of nutrients

The intake of energy and nutrients were all influenced by TF sources ($P < 0.001$; Table 3), and the average daily feed intake (**ADFI**) and daily intake of metabolizable energy (**ME**) were greatest for PKE-fed sows and lowest for SBP- and SH-fed sows. The daily intake of TF, I-NSP, lignin, CP, and lysine were all greatest in PKE-fed sows, whereas MF-fed sows had the lowest intake of TF, I-NSP, and lysine, while SBP-fed sows had the lowest intake of CP. The S-NSP were greatest in SBP-fed sows, and lowest in SH-fed sows, which also had the lowest intake of lignin. Furthermore, the intake of cellulose was greatest in SH-fed sows and lowest in PKE-fed sows.

The ADFI and intake of energy and nutrients were all higher in early gestation as compared with mid-gestation ($P < 0.001$). The ATTD of DM, OM, GE, and NSP was highest for sows fed the SBP diet ($P < 0.001$), and lowest, following the PKE diet ($P < 0.001$) except for ATTD of NSP. The ATTD of NSP was substantially lower for MF (61.4%) as compared with the remaining diets (76.2% to 77.5%; $P < 0.001$). The ATTD of N ranged from 74.6% in the PKE diet to 78.7% in the MF diet ($P < 0.001$). The ATTD of DM, OM, and GE did not differ between gestation periods, whereas the ATTD of NSP was lower in early gestation as compared with mid-gestation (71.6% vs. 74.2%; $P < 0.001$), while the ATTD of N tended to be greater in early gestation as compared with mid-gestation (76.9% vs. 76.2%; $P = 0.07$).

Correlation between ATTDs and intake of fiber components and crude protein

The ATTD of DM, OM, and GE were positively correlated ($P < 0.001$) with daily intake of cellulose and S-NSP (Table 4) and negatively correlated ($P < 0.001$) with daily intake of TF, I-SNP, lignin, and CP; the strongest correlations were found with daily intake of lignin for all three traits ($r = -0.59, -0.66, -0.62$, respectively). The ATTD of N was negatively correlated with daily intake of TF, I-NSP, and lignin ($P < 0.01$) and positively correlated with S-NSP ($P < 0.01$), while it was not correlated with daily intake of cellulose or CP. The strongest correlation for ATTD of N was found with daily intake of I-NSP ($r = -0.53$). The ATTD of NSP was positively correlated with daily intake of TF, cellulose, and I-NSP ($P < 0.05$), and strongest with daily intake of TF and I-NSP ($r = 0.39$), while it was not correlated with daily intake of S-NSP, lignin, or CP.

Table 2. Analyzed chemical composition (as fed) of fiber-rich supplements and experimental diets

		Fiber-rich supplements				Diet			
Item[1]	Basal component	Sugar beet pulp	Soy hulls	Palm kernel expellers	Mixed fiber	Sugar beet pulp (SBP)	Soy hulls (SH)	Palm kernel expellers (PKE)	Mixed fiber (MF)
Chemical composition, g/kg									
DM	867	899	910	917	884	873	874	880	871
Ash	42.3	67.9	58.2	47.5	88.6	46.9	45.0	43.7	51.9
Fat	28.0	28.0	45.0	78.0	56.0	28.0	30.9	41.4	33.8
Starch	488	12	9	12	59	401	406	361	399
TF	114	563	650	597	411	196	213	243	176
S-NSP	28	202	102	62	93	59.7	40.7	36.9	41.4
I-NSP	71	293	494	420	234	111	144	164	105
I-NCP	53	131	210	349	120	68	80	133	67
Cellulose	18	162	284	70	115	44	63	32	38
Ratio I-NSP: S-NSP	2.5	1.4	4.8	6.8	2.5	1.9	3.5	4.4	2.5
Klason lignin	15.1	67.2	54.0	115.8	83.7	25	22	42	29
Enzyme digestible organic matter[2]	921	852	575	499	675	908	861	808	870
GE, MJ/kg	15.3	16.4	16.8	18.9	17.5	15.5	15.6	16.3	15.8
Energy,[3] MJ ME/kg	13.4	10.7	7.9	8.9	10.2	12.9	12.5	12.2	12.8
Energy,[4] MJ ME/kg	13.1	11.6	11.6	9.4	9.7	12.8	12.8	12.1	12.4
Energy,[5] Feed units for sows per kg	1.13	0.80	0.47	0.59	0.74	1.07	1.01	0.98	1.05
Protein and amino acids, g/kg[6]									
CP	116.0 (87.6)	80.0 (49.9)	105.0 (75.3)	148.0 (145.6)	102.0 (30.6)	109.4 (80.8)	114.1 (85.5)	124.6 (103.2)	113.1 (75.8)
Lysine	5.36 (4.2)	4.05 (2.6)	5.71 (4.1)	4.12 (3.9)	5.65 (2.1)	5.12 (3.9)	5.42 (4.2)	5.03 (4.1)	5.42 (3.7)
Lysine:CP ratio, %	4.6 (4.8)	5.1 (5.3)	5.4 (5.4)	2.8 (2.7)	5.5 (7.0)	4.7 (4.8)	4.8 (4.9)	4.0 (4.0)	4.8 (4.9)
Threonine	4.38 (3.3)	3.76 (1.4)	3.56 (2.5)	4.40 (4.0)	4.48 (0.6)	4.27 (2.9)	4.24 (3.2)	4.39 (3.5)	4.40 (2.7)
Leucine	7.80 (5.9)	5.36 (3.9)	5.62 (4.0)	9.39 (7.0)	6.73 (2.3)	7.36 (5.6)	7.42 (5.6)	8.23 (6.2)	7.58 (5.1)
Valine	5.28 (3.8)	4.91 (2.6)	4.61 (3.3)	7.30 (6.1)	5.21 (1.3)	5.21 (5.2)	5.16 (5.4)	5.82 (6.3)	5.27 (4.8)
Methionine	1.94 (1.4)	1.46 (1.1)	1.22 (0.9)	2.73 (2.4)	1.74 (0.7)	1.85 (1.3)	1.82 (1.3)	2.15 (1.7)	1.90 (1.2)
Minerals, g/kg									
Sodium	2.1	0.8	1.3	0.6	0.7	1.9	2.0	1.7	1.8
Potassium	4.9	3.8	11.1	6.1	4.8	4.7	6.0	5.2	4.9
Magnesium	1.2	1.7	2.3	2.6	1.6	1.3	1.4	1.6	1.3
Calcium	7.7	15.1	8.8	6.0	10.0	9.0	7.8	7.2	8.1
Phosphorus	4.2	1.2	2.0	5.3	2.2	3.6	3.8	4.5	3.8
Trace minerals, mg/kg									
Iron	276	498	909	887	614	316	385	440	346
Zinc	120	148	213	159	149	125	136	130	126
Manganese	68	122	133	308	113	78	79	132	77
Copper	19	23	37	43	21	20	22	25	19

[1] ADFI, average daily feed intake; DM, dry matter; GE, gross energy; ME, metabolizable energy; N, nitrogen; NSP, non-starch polysaccharide; S-NSP, soluble non-starch polysaccharide; I-NCP; insoluble non-cellulosic polysaccharides; I-NSP, insoluble non-starch polysaccharide; CP, crude protein.
[2] In vitro enzyme digestible organic matter.
[3] Calculated from Danish feed units (Theil et al., 2020).
[4] Calculated according to EvaPig (2008).
[5] Danish feeding units for sows: Danish feed units are equal to potential physiological energy, which is closely related to net energy (Patience, 2012).
[6] Calculated standardized ileal digestibility values in brackets.

Table 3. Average daily intake of feed and nutrients and apparent total tract digestibility in sows fed four different fiber-rich diets in early (days 0 to 30) and mid (days 30 to 60) gestation[1]

Item[2]	Diet[3]					Gestation period, Per			*P*-value	
	SBP	SH	PKE	MF	SEM	Early	Mid	SEM	Diet	Per
Average daily intake in the period										
ADFI, kg/d	2.41^{c}	2.43^{c}	2.70^{a}	2.52^{b}	0.02	2.73^{a}	2.30^{b}	0.01	<0.001	<0.001
Energy, MJ ME/d	31.1^{c}	30.4^{d}	33.0^{a}	32.2^{b}	0.2	34.5^{a}	28.8^{b}	0.1	<0.001	<0.001
TF, g/d	471^{c}	507^{b}	651^{a}	437^{d}	3.9	538^{a}	495^{b}	3	<0.001	<0.001
S-NSP, g/d	144^{a}	98^{d}	100^{c}	103^{b}	1	117^{a}	105^{b}	1	<0.001	<0.001
I-NSP, g/d	268^{c}	343^{b}	440^{a}	261^{c}	2	341^{a}	315^{b}	2	<0.001	<0.001
I-NCP, g/d	162^{c}	193^{b}	354^{a}	168^{c}	2	230^{a}	209^{b}	1	<0.001	<0.001
Cellulose, g/d	106^{b}	150^{a}	85^{d}	93^{c}	1	111^{a}	105^{b}	1	<0.001	<0.001
Lignin, g/d	59.3^{c}	52.4^{d}	112.4^{a}	72.7^{b}	0.6	77.8^{a}	71.6^{b}	0.4	<0.001	<0.001
CP, g/d	263^{d}	278^{c}	336^{a}	285^{b}	2	315^{a}	266^{b}	1	<0.001	<0.001
Lysine, g/d	12.3^{c}	13.2^{b}	13.6^{a}	13.7^{a}	0.1	14.3^{a}	13.7^{b}	0.1	<0.001	<0.001
Apparent total tract digestibility, %										
DM	84.2^{a}	84.0^{a}	81.2^{b}	81.7^{b}	0.3	82.8	82.7	0.2	<0.001	1.0
OM	87.8^{a}	87.1^{a}	84.1^{c}	85.0^{b}	0.3	86.0	86.0	0.2	<0.001	0.89
GE	86.0^{a}	85.2^{a}	82.6^{c}	83.8^{b}	0.3	84.5	84.4	0.2	<0.001	0.69
N	77.2^{b}	75.8^{c}	74.6^{c}	78.7^{a}	0.4	76.9	76.2	0.3	<0.001	0.07
NSP	77.5^{a}	76.6^{a}	76.2^{a}	61.4^{b}	0.7	71.6	74.2^{a}	0.4	<0.001	<0.001

[1] Data are least square mean values with their standard error of mean (SEM). n = 12 per diet and n = 48 per gestation period (n = 10 and n = 11 for SBP in early and mid, respectively, n = 11 for SH and n = 11 for MF in mid-gestation).
[2] ADFI, average daily feed intake; CP, crude protein; DM, dry matter; OM, organic matter; GE, gross energy; ME, metabolizable energy; N, nitrogen; NSP, non-starch polysaccharide; S-NSP, soluble non-starch polysaccharide; I-NCP; insoluble non-cellulosic polysaccharides; I-NSP, insoluble non-starch polysaccharide; TF, dietary fiber.
[3] SBP, sugar beet pulp; SH, soy hulls; PKE, palm kernel expellers; MF, mixed fiber.
[a,b,c,d] Means within a row with different superscripts differ ($P \leq 0.05$).

Table 4. Correlation coefficients among digestibility and intake of fiber components and crude protein in sows fed four different fiber-rich diets[1] in early (days 0 to 30) and mid (days 30 to 60) gestation

	Apparent total tract digestibility, %					Intake, g/d					
Item[2]	DM	OM	GE	N	NSP	TF	Cellulose	S-NSP	I-NSP	Lignin	CP
DM	1	0.98***	0.97***	0.36***	0.45***	−0.26*	0.55***	0.43***	−0.26*	−0.59***	−0.39***
OM	0.98***	1	0.98***	0.38***	0.42***	−0.35**	0.54***	0.51***	−0.37***	−0.66***	−0.46***
GE	0.97***	0.98***	1	0.48***	0.32**	−0.38***	0.47***	0.50***	−0.41***	−0.62***	−0.43***
N	0.36***	0.38***	0.48***	1	−0.33**	−0.47***	−0.06	0.30**	−0.53***	−0.26**	−0.14
NSP	0.45***	0.42***	0.32**	−0.33**	1	0.39***	0.29*	0.18	0.39***	−0.02	−0.11

[1] Diets: SBP, sugar beet pulp; SH, soy hulls; PKE, palm kernel expellers; MF, mixed fiber.
[2] CP, crude protein; DM, dry matter; GE, gross energy; I-NSP, insoluble non-starch polysaccharide; N, nitrogen; NSP, non-starch polysaccharide; OM, organic matter; S-NSP, soluble non-starch polysaccharide; TF, dietary fiber.
*$P \leq 0.05$; **$P < 0.01$; ***$P < 0.001$.

Sow performance and feed utilization

Backfat gain was highest in MF-fed sows with a mean gain of 0.027 mm/d across early and mid-gestation, while sows fed SH, PKE, and SBP diets on average gained 0.010, 0.014, and 0.008 mm/d, respectively ($P < 0.05$; Table 5). Across all diets, the BF gain tended to be higher in early gestation as compared with mid-gestation ($P = 0.07$).

The ME intake as a percentage of the ME for maintenance was greatest in sows fed the PKE and MF diets (123%), intermediate in sows fed SH (116%), and lowest in SBP-fed sows (114%; $P < 0.01$) and greater in early as compared with mid-gestation (130% vs. 107%; $P < 0.001$).

There was no evidence for differences in BF retention or retention of fat energy as a percentage of retained fat. Retention of fat, protein, and water using the D_2O technique exceeded the observed rate of weight gain by 11% to 32% (Figure 1).

Plasma metabolites

Sows fed the PKE and MF diets had the highest plasma urea concentration (3.65 and 3.34 mmol/L, respectively), whereas it was lower (2.93 and 2.89 mmol/L, respectively; $P < 0.001$; Table 6) for the SBP- and SH-fed sows. The plasma triglyceride concentration (0.60 mmol/L) was highest for PKE-fed sows, intermediate for SBP-fed sows (0.50 mmol/L), and lowest for SH- and MF-fed sows (0.40 to 0.41 mmol/L; $P < 0.001$). Plasma concentrations of NEFA ($P < 0.05$) and triglycerides ($P < 0.01$) were both higher in mid-gestation as compared with early gestation.

Table 5. Initial parameters, performance, and feed utilization in sows fed four different fiber-rich diets in early (days 0 to 30) and mid (days 30 to 60) gestation[1]

	Diet[2]					Gestation period, Per			*P*-value	
Item	SBP	SH	PKE	MF	SEM	Early	Mid	SEM	Diet	Per
Parity	3.5	3.5	3.5	3.5	0.1				0.99	
Sow bodyweight (BW) day 0, kg	261	249	256	253	7				0.65	
Sow backfat (BF) day 0, mm	14.5	14.5	14.7	15.6	1.0				0.85	
Body protein day 0,[3] kg	42.1	40.0	41.3	40.2	1.2				0.51	
Body fat day 0,[3] kg	63.8	62.9	62.7	64.6	3.8				0.98	
Total born piglets, *n*	22.8	21.6	20.1	21.5	2.6				0.81	
Birth weight total litter, kg	26.2	26.6	22.8	26.1	2.5				0.32	
BW gain, g/d	50	212	121	241	77	191	121	50	0.23	0.31
BF gain, mm/d	0.008^{b}	0.010^{b}	0.014^{ab}	0.027^{a}	0.006	0.019	0.010	0.004	<0.05	0.07†
Retained (body) protein,[3] g/d	5	38	16	38	14	31	18	9	0.21	0.29
Retained (body) fat,[3] g/d	33	50	57	62	26	47	53	18	0.85	0.80
Retained protein energy, MJ/d	0.1	0.9	0.4	0.9	0.3	0.7	0.4	0.2	0.21	0.29
Retained fat energy, MJ/d	1.3	2.0	2.3	2.5	1.0	1.9	2.1	0.7	0.85	0.80
Retained energy, MJ/d	1.4	2.9	2.7	3.4	1.2	2.6	2.5	0.8	0.67	0.94
Retained energy,[4] % of ME$_{Intake}$	4.7	9.8	7.9	10.5	3.8	7.5	8.9	2.6	0.68	0.69
ME required for maintenance,[5] MJ/d	28	26	27	26	0.5	27	27	0.3	0.26	0.57
ME intake, relative to maintenance requirement, %	114^{b}	116^{ab}	123^{a}	123^{a}	2.4	130^{a}	107^{b}	1.5	<0.01	<0.001

[1] Data are least square mean values with their standard error of mean (SEM). *n* = 12 per diet and *n* = 48 per gestation period (*n* = 10 and *n* = 11 for SBP in early and mid, respectively, *n* = 11 for SH and *n* = 11 for MF in mid-gestation).
[2] SBP, sugar beet pulp; SH, soy hulls; PKE, palm kernel expellers; MF, mixed fiber.
[3] Retained protein and fat, calculated from the deuterium oxide (D_2O) dilution technique.
[4] Retained energy as protein: retained protein × 23.9 MJ/kg and retained energy as fat: retained fat × 39.8.
[5] Metabolizable energy (ME) for maintenance, calculated as: 0.420 MJ/d per sow BW^0.75 (Theil et al., 2020).
^{a,b}Means within a row with different superscripts differ ($P \le 0.05$).
†means tends to be different ($0.05 < P \le 0.10$).

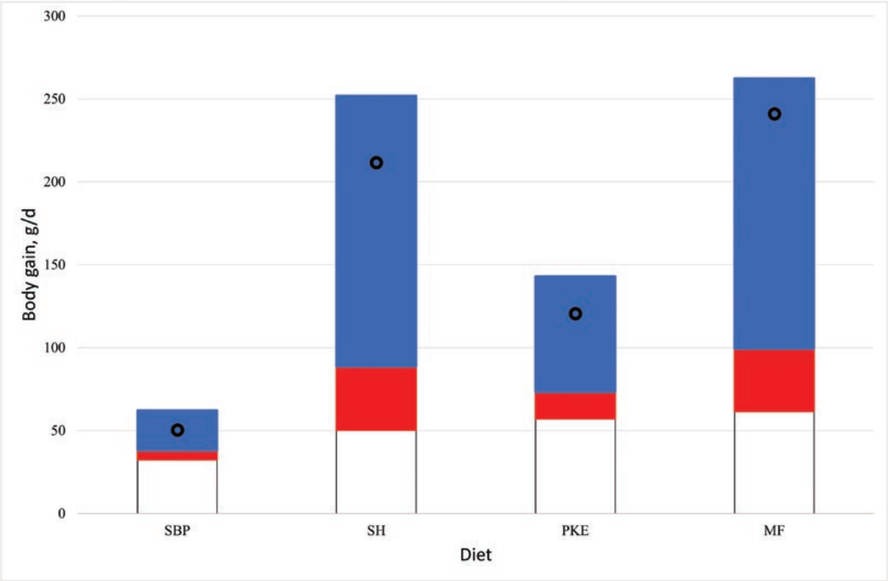

Figure 1. Gain of retained water (blue bar), protein (red bar), fat (white bar), and total body weight (black circles) in sows fed four different fiber-rich diets throughout gestation. Protein and fat gains were calculated from the deuterium oxide dilution technique and assuming that retained muscle contains 4.2 g of water and minerals per g of protein and that fat of contains 0.17 g of water per g of fat (Noblet and Etienne, 1987) in sows fed four different fiber-rich supplements. SBP, sugar beet pulp; SH, soy hulls; PKE, palm kernel expellers; MF, mixed fiber, in early (days 0 to 30) and mid (days 30 to 60) of gestation (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

Balances of N and GE

The N intake ($P < 0.001$) and N retention ($P < 0.05$) were highest for PKE-fed sows and lowest for SBP-fed sows (Table 7). In contrast, SBP-fed sows had the highest urinary N output as a percentage of their N intake (63%) while it was lowest for sows fed SH and PKE diets (both amounted to 50%; Figure 2).

The PKE-fed sows had the highest ME intake (MJ ME/d) of 37.8 MJ/d, due to the largest feed intake, while the SH- and

Table 6. Plasma metabolites in sows fed four different fiber-rich diets at days 30 and 60 of gestation[1]

Item	Diet[2]					Gestation day, day			*P*-value	
	SBP	SH	PKE	MF	SEM	30	60	SEM	Diet	Day
Nonesterified fatty acids, µekv./L	58.5	62.3	62.2	50.8	6.7	49.9^{b}	67.1^{a}	4.7	0.55	<0.05
Glucose, mmol/L	4.37	4.40	4.32	4.29	0.10	4.26	4.43	0.07	0.84	0.07
Urea, mmol/L	2.93^{b}	2.89^{b}	3.65^{a}	3.34^{a}	0.11	3.30	3.10	0.08	<0.001	0.07
Lactate, mmol/L	1.71	2.03	1.81	2.10	0.21	1.98	1.85	0.15	0.48	0.54
Triglyceride, mmol/L	0.50^{b}	0.41^{bc}	0.60^{a}	0.40^{c}	0.03	0.43^{b}	0.52^{a}	0.02	<0.001	<0.01

[1] Data are least square mean values with their standard error of mean (SEM). $n = 12$ per diet and $n = 48$ per gestation period ($n = 10$ and $n = 11$ for SBP in early and mid, respectively, $n = 11$ for SH and $n = 11$ for MF in mid-gestation).
[2] SBP, sugar beet pulp; SH, soy hulls; PKE, palm kernel expellers; MF, mixed fiber.
[a,b,c] Means within a row with different superscripts differ ($P \leq 0.05$).

Table 7. Realized nitrogen (N) and gross energy (GE) intake, output, and total retention in sows fed four different fiber-rich diets at days 30 and 60 of gestation[1]

Item	Diets[2]					Gestation day, day			*P*-value	
	SBP	SH	PKE	MF	SEM	30	60	SEM	Diets	Day
Feces production, kg DM/d	0.34^{b}	0.35^{b}	0.45^{a}	0.42^{a}	0.01	0.39	0.39	0.01	<0.001	0.98
Feces N, g/kg DM	29.1^{c}	32.5^{a}	30.5^{b}	24.2^{d}	0.3	28.7^{b}	29.5^{a}	0.2	<0.001	<0.01
Urine production, kg/d	22.2	25.7	21.0	24.7	3.9	23.7	23.1	2.7	0.81	0.88
Urine N, g/100 g	0.17	0.13	0.21	0.17	0.03	0.17	0.17	0.02	0.21	0.98
Urine pH	7.03^{ab}	7.19^{a}	6.82^{b}	7.05^{a}	0.07	7.08	6.97	0.05	<0.01	0.11
Average heart rate, bpm	93.1	90.6	89.6	99.5	4.9	94.3	92.1	3.3	0.38	0.63
Realized N intake, g/d	43.0^{d}	45.0^{c}	55.1^{a}	47.2^{b}	0.6	52.9^{a}	42.2^{b}	0.4	<0.001	<0.001
Urine N output, g/d	27.1^{ab}	22.3^{b}	27.7^{a}	27.9^{a}	1.6	26.9	25.6	1.2	<0.05	0.43
Fecal N output, g/d	9.9^{c}	11.0^{b}	14.0^{a}	10.1^{c}	0.2	12.3^{a}	10.2^{b}	0.2	<0.001	<0.001
Total N retention,[3] g/d	6.0^{b}	11.4^{a}	12.8^{a}	9.0^{ab}	1.7	13.3^{a}	6.3^{b}	1.2	<0.05	<0.001
GE intake, MJ/d	38.0^{d}	43.0^{c}	50.2^{a}	46.1^{b}	0.6	49.2^{a}	39.5^{b}	0.4	<0.001	<0.001
Urine GE output,[4] MJ/d	1.4^{ab}	1.1^{b}	1.4^{a}	1.4^{a}	0.1	1.4^{a}	1.3^{b}	0.1	<0.05	0.43
Fecal GE output, MJ/d	5.9^{c}	6.3^{c}	8.6^{a}	7.3^{b}	0.1	7.8^{a}	6.3^{b}	0.1	<0.001	<0.001
Methane GE output,[5] MJ/d	0.3^{b}	0.3^{b}	0.4^{a}	0.2^{c}	0.0	0.4^{a}	0.3^{b}	0.0	<0.001	<0.001
Metabolizable energy,[6] MJ/d	30.4^{c}	35.3^{c}	39.8^{a}	37.0^{b}	0.5	39.7^{a}	31.6^{b}	0.4	<0.001	<0.001
Total heat production,[7] MJ ME/d	27.5	26.9	26.5	28.8	1.5	27.5	27.3	1.0	0.63	0.89
Total energy retention,[8] MJ/d	3.3^{c}	8.2^{b}	13.3^{a}	7.8^{bc}	1.6	12.2^{a}	4.1^{b}	1.1	<0.001	<0.001

[1] Data are least square mean values with their standard error of mean (SEM). $n = 12$ per diet and $n = 48$ per gestation period ($n = 10$ and $n = 11$ for SBP in early and mid, respectively, $n = 11$ for SH and $n = 11$ for MF in mid-gestation).
[2] SBP, sugar beet pulp; SH, soy hulls; PKE, palm kernel expellers; MF, mixed fiber.
[3] N intake – (Urine N output + Fecal N Output).
[4] Assuming that energy in urine from sows contains 50.41 kJ/g N (Theil et al., 2002a, 2004).
[5] 0.0628 + 0.00488 × fermented fiber, g/kg DM (Jørgensen et al., 2011).
[6] GE intake – (urine GE output + methane GE output + feces GE output).
[7] Calculated using the heart rate and heat production relationship (Krogh et al., 2018).
[8] ME intake – HP total.
[a,b,c,d] Means within a row with different superscripts differ ($P \leq 0.05$).

SBP-fed sows had the lowest intake of ME (33.8 and 28.5 MJ/d, respectively; $P < 0.001$). The PKE-fed sows showed the highest energy retention (13.3 MJ/d), while the other treatments ranged between 3.3 and 8.2 MJ/d ($P < 0.001$). The SBP-fed sows had the highest urine GE output (3.7%) as a percentage of GE intake (Figure 3), intermediate for PKE- and MF-fed sows (2.8% and 3.0%, respectively), and lowest in SH-fed sows (2.6%). The HP as a percentage of GE intake was highest for SBP-fed sows (72.4%), intermediate for SH- and MF-fed sows (62.4% and 62.5%, respectively), and lowest for PKE-fed sows (52.8%).

Gross energy intake, ME output, and total energy retention were greater in early gestation as compared with mid-gestation. Both total N and total energy retention were greater in early gestation as compared with mid-gestation ($P < 0.001$).

Discussion

Fiber sources and energy digestibility

Energy loss through feces amounted on average to 15.8% of the total GE intake in both gestation periods and ranged from 14.5% to 17.4% across all four fiber-rich diets, despite that sows were fed up to 24.3% TF on a DM basis. Compared with growing pigs, sows have a higher fermentation

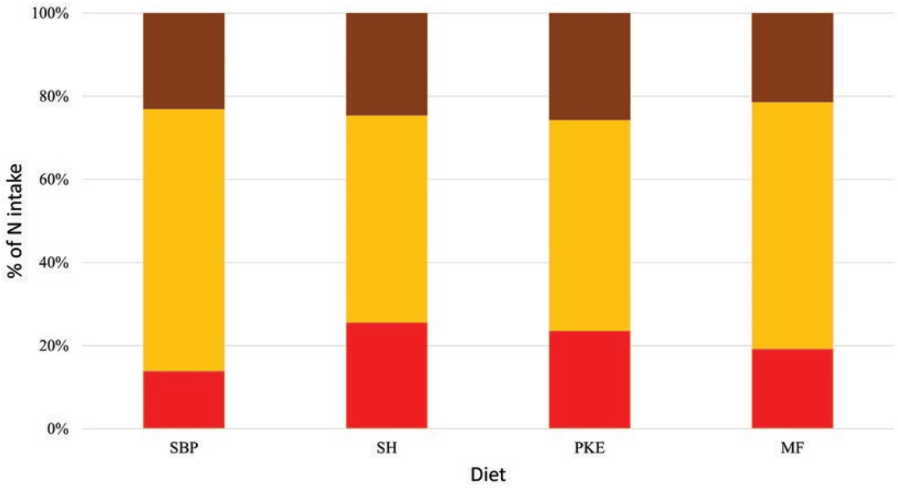

Figure 2. Fecal (brown bar) and urine (yellow bar) nitrogen (**N**) output, and N retention (red bar) as percentage of N intake in sows fed four different fiber-rich supplements. SBP, sugar beet pulp; SH, soy hulls; PKE, palm kernel expellers; MF, mixed fiber, in early (days 0 to 30) and mid (days 30 to 60) of gestation (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

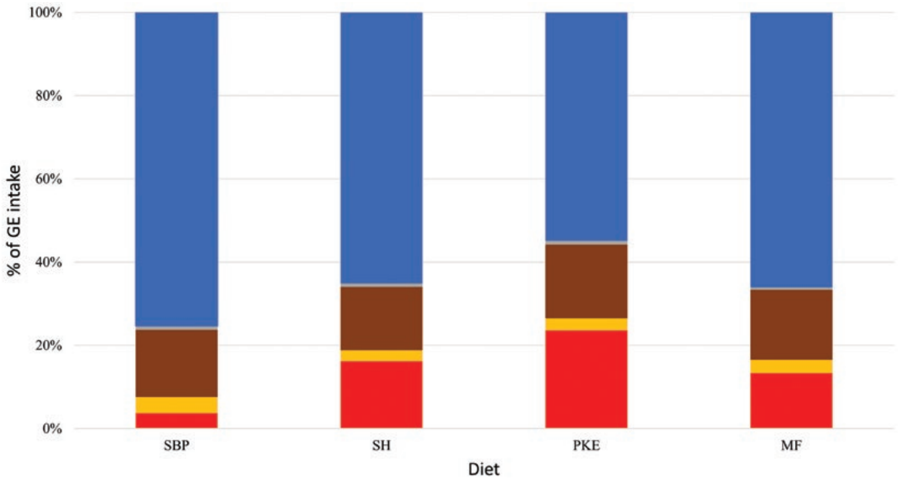

Figure 3. Heat energy (blue bar), methane energy (gray bar), fecal gross energy (**GE**) output (brown bar), urine GE output (yellow bar), and GE retention (red bar) as percentage of GE intake in sows fed four different fiber-rich supplements. SBP, sugar beet pulp; SH, soy hulls; PKE, palm kernel expellers; MF, mixed fiber, in early (days 0 to 30) and mid (days 30 to 60) of gestation (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

capacity and are therefore more efficient in degrading fibers than growing pigs (Fernández et al., 1986). However, the superiority of sows in fermenting fiber compared with growing pigs still depends on the fiber type (Noblet and Le Goff, 2001; Jørgensen et al., 2007), emphasizing that trials should be carried out to specifically measure the energy value of TF for sows. Noblet and Le Goff (2001) reported digestibility coefficients for hemicellulose and acid detergent fiber (cellulose + lignin) and found acid detergent fiber to differ the most between sows and growing pigs. Sows had on average 14% units higher digestibility of acid detergent fiber than growing pigs, while hemicellulose were only 6% units higher for sows. For more concentrated diets the difference in the digestibility of energy and nutrients in sows and growing pigs is smaller because a larger part of the digestion is caused by endogenous enzymes in the small intestine (Noblet and Le Goff, 2001; Jørgensen et al., 2007). Therefore, the energy and nutrient digestibility of fiber-rich diets will differ substantially between sows and growing pigs depending on the fiber sources. For instance, Noblet and Le Goff (2001) found that sows fed SBP had 7% units higher energy digestibility as compared with growing pigs, while it was 24% units higher in sows when fed SH. The main reason for the higher digestibility of TF in sows than in growing pigs is, firstly, that sows have a greater and more developed hindgut causing a longer retention time (Jha and Berrocoso, 2015). Secondly, sows are fed close to maintenance in early and mid-gestation (SEGES, 2019b), whereas growing pigs are fed ad libitum, which corresponds to approximately 3-fold their energy requirement for maintenance (Jørgensen et al., 2011). Sufficient time for fermenting fibers in the hindgut seems to be important to achieve a high digestibility of fibers, especially when animals are fed high-fiber diets. In support of the impaired energy digestibility with increasing feed intake, Zhou et al. (2018) found a decrease of 1.6% units in GE digestibility from day 3 to day 17 in lactating sows, when ADFI increased from 3.8 kg/d in wk 1 to 8.1 kg/d in wk 3 of lactation.

Fiber components, energy, and organic matter digestibility

The high ATTD of energy following the SBP and SH diets in the present study is most likely associated with the high proportion of soluble NSP and the low degree of lignification. In line with that, Renteria-Flores et al. (2008) and Serena et al. (2008) found that energy digestibility was greater if the TF fraction was rich in soluble fiber as compared with insoluble fibers. Lignin is considered indigestible and is sometimes used as an intrinsic marker in digestibility studies (Jagger et al., 1992). In plants, the lignin content increases with the age or developmental stage and the lignification process as plants mature, which is known to considerably reduce the energy digestibility and overall nutritional value of the plant when used in animal feeds (Surendra and Khanal, 2015). Processing of co-products increases the proportions of outer layers (hulls and bran fractions) and hence lignin content. In this study, strong negative correlations between nutrient digestibilities and daily lignin intake were found, and emphasized that lignin compromises the digestibility of nutrients. In a recent study with growing pigs and sows, the digestibility of palm kernel meal added to a corn-based diet was studied, and GE digestibility of 80.5% and 82.1%, respectively, were found (Dong et al., 2020). The ATTD of GE for sows was thus fairly close to what is found in the present study.

Sugar beet pulp is in general a very good fiber source for sows (Bach Knudsen, 1997; Renteria-Flores et. al., 2008; Priester et al., 2020) as the energy digestibility is high (Jørgensen et al., 2007). The SBP is characterized by a high concentration of soluble fiber and low concentration of lignin, as found in the present study, and is therefore often a preferred fiber source for gestating sows. Compared with the SBP diet, the ATTD of energy and NSP of the SH diet was almost as high, whereas the ATTD of energy in the MF diet was lower than in SBP- and SH-fed sows. This was the case even though the SBP fraction made up a high proportion of the MF supplement. However, the oat hulls and OptiCell are two ingredients, which limit the energy digestibility. A previous study has also shown that oat hulls decrease energy digestibility as compared with SH (Stanogias and Pearcet, 1985; Mateos et al., 2007). The ATTD of energy in the SBP, SH, PKE, and MF diets were 3.3% units to 5.0% units lower than reported by Feyera et al. (2021) in late gestating sows fed the same type of fiber-rich supplements. The values in the latter study were higher, which may be explained by the replacement of 29% of the gestation feed with a common lactation feed low in fiber and with higher ATTD of energy.

The in vitro enzyme digestibility of OM was fairly close to its in vivo digestibility. For the SBP and MF diets, it was slightly higher (3.1% units and 2.0% units, respectively), whereas it was slightly lower the in SH and PKE diets (−0.9% units and −3.3% units, respectively) as compared with in vivo digestibility. This supports that the in vitro digestibility fairly well predicts the energy value of sow diets, whereas the energy value of the fiber-rich ingredients is less accurately predicted.

Heat production and energy utilization

The greatest loss of energy in pigs and in sows particularly, is inevitable due to their HP. For gestating sows, energy required for maintenance, which includes digestive, absorptive and cellular metabolic processes, minimal physical activity, and thermoregulation (Ramonet et al., 2000; Theil et al., 2020). In addition to maintenance, heat is produced due to anabolic processes (maternal and fetal growth), thermoregulation, oxidation of excess dietary amino acids, and physical activity above the minimum included in the concept of maintenance.

When sows are fed at or below maintenance, the HP deriving from the hindgut due to fermentation is beneficial, as it contributes to maintain a constant body temperature, which may reduce oxidation of nutrients for thermoregulation. Thus, fermentable fibers may therefore be more valuable for sows than for growing pigs (Noblet and Le Goff, 2001; Olesen et al., 2001). Particularly when sows are kept outdoor in winter conditions (Eskildsen et al., 2020) or when sows are fed at or below maintenance in gestation. In contrast, fermentation heat has no value for the animal with respect to thermoregulation in growing pigs and lactating sows as they are fed 3- to 4-fold above their maintenance requirement and therefore produces huge amounts of heat (Theil et al., 2020).

In the current study, the total HP estimated from heart rate did not differ between treatments and was between 26.5 and 28.8 MJ/d. This is in line with previous studies with early and mid-gestating sows, where HP was reported to be 25.9 to 28.9 MJ/d when sows were fed increasing levels of fibers from SBP (Wisbech et al., 2022) and 26.4 to 28.0 MJ/d in gestating sows fed control and fibrous mixed diet in early and mid-gestation (Olesen et al., 2001). Lower HP was reported by Theil et al. (2002b), for early and mid-gestating second parity sows fed high and low dietary protein, with HP values ranging from 21 to 23 MJ/d. The lower HP values in the latter study are most likely due to lower BW (187 to 194 kg) and a lower DM intake (1.68 kg/d) as compared with the present study (249 to 261 kg BW; 2.30 to 2.73 kg/d ADFI). Previously, it has been shown that diets high in soluble fiber decrease physical activity (Rijnen et al., 2003; Jørgensen et al., 2010), which in turn reduces the total HP. In line with that, Jørgensen et al. (2010) reported that sows fed diets with high inclusion rates of either potato pulp or SBP, both high in soluble fiber, lowered the physical activity, as compared with sows fed diets with high contents of insoluble fiber or a low fiber control diet. Soluble fibers are known to swell to a larger extent than insoluble fibers (Zhou et al., 2018) with the consequence of increasing the gut fill, which may play a role in signaling satiety through the activation of stretch receptors (Paintal, 1954). However, according to the heart rate results, the present study did not indicate an attenuating effect of SBP or any of the other fiber sources on physical activity.

Fiber sources and digestibility and utilization of nitrogen

The ATTD of N was lower for all fiber-rich diets and clearly lower than normally found in common gestation diets with low fiber content. The basal component used in this study was almost identical to the low-fiber diet reported by Wisbech et al. (2022), where the ATTD of N was 82.2% in both early and mid-gestation. Supplying the fiber-rich supplements on top of the basal component reduced the ATTD of N, most pronouncedly in the PKE diet (74.6%) in response to inclusion of 24% to 29% in the total diet. For the three other fiber-rich diets, the ATTD of N dropped less and amounted 75.8% to 78.7%. Thus, inclusion of more fiber in the diet clearly reduced the ATTD of N, although it depended on the fiber sources. A recent study with late gestating sows (Feyera et al., 2021) fed the same fiber-rich ingredients as in the present study showed higher ATTD of N (82.3% to 86.5%), which was due to inclusion of soybean meal in the transition diet. In the current study, a negative correlation between ATTD of N and I-NSP was found, as it was also reported in the experiment with late gestating sows (Feyera et al., 2021). This negative correlation between I-NSP and N digestibility has previously been reported by Février et al. (2001), where the ileal digestibility of amino acids in three batches of both palm kernel meal and cotton seed meal were investigated in pigs. Especially the ileal digestibility of lysine was negatively correlated with I-NSP content and in the analysis of cotton seed meal, the authors reported a cumulative negative effect of heat treatment during processing of cotton seed meal. The study was based on a small sample size (three), which according to the authors, might have been too low, due to a high botanical diversity and variation in technological processing across batches.

The calculated retention using the N balances overestimated the total weight gain of sows in the present study, which most likely is due to the short collection period of urine (approx. 6 h). Thus, the data suggest that the urine bladder was not completely emptied when urine was collected, whereby the N retention as estimated from the difference between input and output, was overestimated. This has only minor consequences for the estimated energy balances, as the impact of N on energy loss in urine is relatively low, whereas it is much more important when estimating the N balances, where N secreted through urine accounts for most of the N loss. In this context it is worth noticing that estimating N balances by subtracting output from intake, results in retention including all errors and when retention is low, errors will impact the result relatively more. In the current study, we used the D_2O method to estimate BW gain and composition and compared it to a direct estimate of BW gain. The difference between measured BW gain and estimated BW gain using the D_2O method is in line with our own previous results, which indicated a 6% to 36% overestimation of BW when using the D_2O method (Wisbech et al., 2022) and with the greatest deviation when BW gain was lowest. A limitation of the D_2O method is that it relies on a precise detection of fat and protein gain for the detection of BW gain, which can be problematic when the balance is close to zero. Van Vliet et al. (2016) showed a detection limit of 1% for changes in body fat pool and 0.2% as the detection limit for changes in protein pool using the D_2O method.

The PKE-fed sows showed the second lowest N retention, when applying the D_2O method, despite having the highest CP intake. This may potentially be explained by heat damage of the PKE protein during processing, since heat treatment is known to cause a Maillard reaction. Oliveira et al. (2021) investigated the relationship between heat processing and AA damage and found that a lysine:CP ratio below 3% could indicate heat damage. In the current study, the PKE diet had a lysine:CP ratio of 2.8%, which was lower than the basal component and also lower than the three other fiber-rich supplements, with ratios in the range of 4.6% to 5.5%. These data, combined with the highest urea plasma concentration, compared to SBP and SH, support our speculation, that the protein originating from PKE was likely damaged during processing and resulted in poor protein quality. Moreover, PKE has a high content of arginine compared to the other ingredients, and it may compete with lysine to be transported across the intestinal wall (Stein et al., 2015). Therefore, we speculate that sows fed the PKE diet may have suffered from insufficient lysine uptake to portal blood, which in turn could limit the N retention. However, the PKE diet resulted in the highest calculated N and energy retention. This could potentially be an overestimation since the PKE pellet quality was rather bad and therefore spilled PKE may not have been accounted for when feed leftovers were recorded.

Conclusion

This study showed that early and mid-gestating sows fermented all four fiber-rich diets efficiently, with ATTD energy values above 82%, whereas the ATTD and utilization of N were compromised by the fiber-rich ingredients. Across the diets, the ATTD of energy was most strongly negatively correlated with lignin, whereas ATTD of N was strongest correlated with I-NSP. The study did not support SBP as a superior fiber source for gestating sows as compared with other fiber sources, probably due to the low feeding level in gestation and the very high ATTD of energy for all four fiber-rich diets.

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Conflict of Interest Statement

The authors declare that there are no conflict of interest.

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5.6. Paper III

Influence of fiber-rich co-products on nutrient and energy digestibility and utilization in sows.

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Non ruminant nutrition

Influence of fiber-rich coproducts on nutrient and energy digestibility and utilization in sows

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Abstract

Coproducts from the food and agricultural industries can potentially be used to replace concentrated high-value grain crops in diets for sows. The coproducts are typically high in fiber and with diverse composition. Energy digestibility and utilization are generally high in sows fed fiber-rich feedstuff, but nitrogen digestion and utilization may be compromised. The purpose of this study was to quantify the apparent total tract digestibility (**ATTD**) of nutrients and utilization of energy and nitrogen in empty nonlactating sows fed with six different fiber-rich coproducts (**FRCP**). Brewers spent grain (**BSG**), pea hull (**PH**), potato pulp (**PP**), pectin residue (**PR**), sugar beet pulp (**SBP**), and seed residue (**SR**) were mixed into a basal diet (**BD**) with as high an inclusion level as possible, or the BD was fed solely to eight empty sows in a Youden square incomplete cross-over design. The collection period consisted of a total collection period of 5 d, of which 2 d were in a respiration chamber. The sows had a gross energy (**GE**) intake between 28.5 and 42.3 MJ/d; greatest for the PH fed sows and lowest for the PP fed sows. The ATTD of dry matter, organic matter, GE, and N did not differ among the BD and the PH and SBP fed sows, while the ATTDs of all nutrients and energy were intermediate for PR and BSG lowest in SR fed sows ($P < 0.01$). The differences were caused by variation in digestible and metabolizable energy content of the FRCP ingredients, which was lowest for SR, intermediate for PR followed by BSG and greatest for SBP, PP, and PH ($P < 0.001$). Total heat production (**HP**) did not differ among treatments but the nonactivity related HP was highest in SR fed sows and lowest in PH and SBP fed sows ($P < 0.05$). Retention of energy was greatest following the PH and BD (7.42 and 2.19 MJ/d, respectively), intermediate for PP, SBP, and BSG fed sows (−0.22 to −0.69 MJ/d) and lowest for the PR and SR fed sows (−4.26 and −6.17 MJ/d, respectively; $P < 0.001$). From a sow feeding perspective, SBP and PH have the potential to partly replace high-value grain crops due to high ATTD of all nutrients and because sows can efficiently utilize energy and protein. In contrast, SR and PR show low ATTD of nutrients and energy, thereby compromising the nutritive value. PP and BSG also have the potential to be included in sow diets, but caution should be taken because of compromised N utilization and thereby increased environmental impact.

Lay Summary

Coproducts from the food and agricultural industries have the potential to partly substitute grain in diets for empty nonlactating sows. Many coproducts are high in fiber and with diverse fiber composition. Some being easily fermented, while others are more resistant to fermentation giving rise to a large variation in the total tract digestibility and utilization of nutrients and energy. How well fiber-rich coproducts are digested and utilized is poorly understood in sows, but it is important to ensure an optimal energy and protein composition of the feed depending on the physiological stage of the sow. This study aimed to increase knowledge on the digestibility and utilization of six fiber-rich coproducts potentially to be included in the sow's feed. We found pea hulls and sugar beet pulp suitable as grain replacers due to their high total tract digestibility and no negative effects on energy and protein utilization. Potato pulp and brewers spent grain were also well suited. However, caution should be taken in balancing diets because of increased fecal and urine nitrogen output, which will increase environmental impact. Seed and pectin residues primarily serve as gut fill.

Keywords: feed efficiency, gut fill, heat production, nitrogen utilization, sow nutrition

Abbreviations: ATTD, apparent total tract digestibility; BD, basal diet; BSG, brewers spent grain; BW, body weight; C, Carbon; CO2, carbon dioxide; cTF, calculated total fiber; DM, dry matter; FRCP, fiber-rich coproduct; GE, gross energy; HP, heat production; I-NCP, insoluble noncellulosic polysaccharides; ME, metabolizable energy; N, nitrogen; NSP, nonstarch polysaccharides; OM, organic matter; PH, pea hull; PP, potato pulp; PR, pectin residue; SBP, sugar beet pulp; S-NCP, soluble noncellulosic polysaccharides; SR; seed residue, TF, total fiber

Introduction

Coproducts from the vegetable food and agricultural industries are present throughout Europe in reasonable quantities, for example, from the processing of grains, roots, and tubers such as brewers spent grain (**BSG**), sugar beet pulp (**SBP**), and potato pulp (**PP**). Additionally, coproducts may also be available more locally from processing of citrus peel and peas and sifting of ryegrass seed, in the form of pectin residue (**PR**), pea hull (**PH**), and seed residue (**SR**).

The replacement of high-value crops, such as grain, with coproducts, without compromising animal health, well-being, and production, is the key factor in the transition to a more circular economy (Puente-Rodríguez et al., 2022). A common feature of these coproducts is that they are high in total fiber with a diverse composition and varying properties of nonstarch polysaccharides (**NSP**) in terms of solubility and degree of lignification (Serena and Knudsen, 2007). This has a significant influence on the total tract digestibility of

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nutrients and energy (Serena et al., 2008b). Lactating sows (Zhou et al., 2018) have a high feed intake to support the high energy demand, whereas dry sows are fed less due to their lower demand for energy. This makes dry sows obvious candidates for utilizing fiber-rich coproducts (**FRCP**). Fiber-rich coproducts may enhance fermentation in the hindgut (Jha and Berrocoso, 2015) and thereby promote the production of short-chain fatty acids, which can be efficiently utilized during gestation, especially if the sow needs to retain fat. The ketogenic short-chain fatty acids, acetate and butyrate, are expected to be more suitable as precursors for de novo fatty acid synthesis than glucose because two of six carbons are lost as CO_2 when glucose is used as a precursor (Theil et al., 2020). However, the energy and protein utilization of fiber-rich feedstuffs in sows are generally not well studied and understood (Slama et al., 2019). In a recent study, an energy digestibility above 82% in four high-fiber diets fed to gestating sows was found (Wisbech et al., 2023), but the N digestibility was compromised depending on the fiber source. An associated effect of increased fermentation of fiber may be a shift in N excretion from urine to feces and increased production of enteric methane (Bindelle et al., 2008; Vu et al., 2009). Additionally, increased gut fill and a larger proportion of energy deriving from SCFA (Serena et al. 2008a, 2009) may reduce the aggressive and stereotypic behavior of the sows (Priester et al., 2020) making sows less physically active, partly due to increased long term physical filling and satiety (Rijnen et al., 2003; Jørgensen et al., 2010). These factors may contribute to reduced overall energy needs by the sows.

The main factor influencing the energy value of fiber-rich feedstuff is the digestibility of the energy (Just, 1982; Beecher et al., 2015). This is linked to the composition of the NSP fraction and the degree of lignification characterized by the polyphenolic lignin cross-link to the NSP (Bach Knudsen et al., 2017). This polysaccharide-lignin cross-link makes the whole matrix structure rigid and more or less resistant to microbial degradation (Ruiz-Dueñas and Martínez, 2009). However, sows have a higher fermentative capacity than growing-finishing pigs (Che et al., 2011; Li et al., 2019), resulting in higher total tract digestion of nutrients and energy (Fernández et al., 1986; Noblet and Shi, 1993; Jørgensen et al., 2007; Jacyno et al., 2016).

The current study was performed to investigate total tract digestibility of nutrients and energy, energy utilization and influence on gas and HP in sows fed high levels of FRCP with contrasting fiber composition and lignification. BSG, PP, PR, and SBP, all provided in wet form, and SR and PH in dry form were used. The FRCP were added to a **BD** in as high an amount as possible. It was hypothesized that the digestibility and utilization of energy and nutrients in FRCP would differ, mainly due to differences in nonstarch polysaccharide composition and degree of lignification.

Materials and Methods

The present experiment complied with the Danish Ministry of Justice Law number 382 (June 10, 1987). Act number 726 (September 9, 1993, as amended by act number 1081 on December 20, 1995), concerning experiments with and the care of animals.

Experimental design, animals, and housing

A total of eight first and second parity, empty nonlactating, sows were used in a Youden square incomplete cross-over design study with 4 to 6 replicates per FRCP and 7 replicates of the BD. Sows were weaned after a 28-d lactation period, were not rebred, and included in the study after 3 wk. The study was performed in two blocks and an additional follow-up block. Block one consisted of four sows, of which two of the four continued in block two together with two new sows. Due to the high refusal rate of the feed, independent of diet, for the two omitted sows in block one, it was necessary to conduct a follow-up block with two additional sows. The feed left over of all other sows was low and independent of diet.

Each experimental period consisted of an adaptation period of 14 d, where the sows were housed individually in 8 m^2 pens with concrete floors and fed the experimental diet, followed by 5 d of total collection in metabolic cages. During the collection period, day two and three (total of 48 h) of collection was performed in one of two (A or B) respiration chambers.

The body weight was recorded before and after the sow was placed in the metabolic cage.

The total amount of feed for each animal was split in two equal size portions and fed twice daily (0800 and 1500 hours) and the light was turned on 0600 to 1800 hours. Temperature (18.2 ± 1.2 °C) and humidity (57.7% ± 11.5%) were kept constant in the respiration chambers and similar to the temperature metabolic cages. The respiration chambers used to estimate the gas exchange were open air circuit chambers, as described by Jørgensen et al. (1996).

Feces and urine were collected daily and weighed. All feces and an aliquot of urine (10% of the daily production) were kept at 5 °C until the end of the collection period. Urine was continuously mixed with 5% sulphuric acid to prevent evaporation of N through volatilization of ammonia (NH_3). At the end of the collection period, subsamples of the pooled urine and feces were obtained and stored at −20 °C until analysis.

Positioning of the sows (standing/lying) was recorded with a photocell (OA 722 NPN/PNP, T.J.C. Teknik aps, Virum, Denmark) during the 2 d in the chambers and activity was measured with passive infrared detectors and a signal-processing interface (Pedersen and Pedersen, 1995) when the sows were in the respiration chamber.

Diets

The sows were fed either the BD, which complied with the Danish nutrient recommendations (Danielsen, 1998), or a reduced amount of the BD combined with one of six dry or wet FRCP. The dry coproducts were PH (Prodana Seeds A/S, Odense, Denmark) or ryegrassSR (DLF Trifolikum A/S, Roskilde, Denmark). The wet coproducts were BSG (Carlsberg A/S, Fredericia, Denmark, delivered by Agro-Korn A/S, Videbæk, Denmark), PR (CP Kelco aps, Lille Skensved, Denmark), PP (KMC, Kartoffelmelcentralen Amba, Brande, Denmark), and SBP (Danisco Sugar A/S, Assens, Denmark). The BD and FRCP were weighed individually and then mixed in the trough when fed. Inclusion of the FRCP was as high as possible, but restricted to an amount where the trough was emptied within an hour after feeding. Adjustments in inclusion rates of FRCP were made within the first 2 d of the adaptation period, where the inclusion level, for each sow, was fixed for the rest of the adaptation and subsequent collection period. The degree of variation in FRCP inclusion among sows receiving the same FRCP was within approximately 25%. If any, the feed left over, was collected daily.

Representative samples of BD and FRCP for analysis were sampled at the start of the collection periods. Dry samples were stored at room temperature, whereas the wet ones were stored at −20 °C until later analysis.

Chemical analysis

All feed and fecal analyses were performed in duplicate, and samples were analyzed for dry matter (**DM**), gross energy (**GE**), nitrogen (**N**), sugars, starch, nonstarch polysaccharides (**NSP**), Klason lignin and carbon (**C**). DM was determined by drying the material at 103 °C for 20 h to constant weight, GE was determined by a LECO AC 300 automated calorimeter system (LECO, St. Joseph, MI, USA), ash and N according to AOAC (1990), where N was analyzed with the Kjeldahl method on a KjelTecTM 2400 (Foss, Hillerød, Denmark) and crude protein calculated as N × 6.25. Sugars, starch, and NSP separated into soluble noncellulosic (**S-NCP**) and insoluble noncellulosic polysaccharides (**I-NCP**) and cellulose were analyzed according to Bach Knudsen (1997). Klason lignin was determined as the residue after hydrolysis of the insoluble fraction by 2 mol/L of H_2SO_4 (Theander and Åman, 1979). Carbon was analyzed described by Neergaard et al. (1969).

Calculations and statistical analysis

Apparent total tract digestibility (ATTD) of nutrients and energy in the diets has been calculated, with N as an example, as follows:

$$\text{ATTD N } [\%] = \frac{\begin{array}{c}(\text{Diet N } [\%] \times \text{diet intake } [\text{kg/d }] \\ -\text{ Fecal N}[\%] \times \text{fecesproduced } [\text{kg/d }])\end{array}}{\text{Diet N}[\%] \times \text{diet intake}[\text{kg/d}]} \times 100,$$

and the ATTD of the FRCP was calculated using the difference method, with N as example, as follows:

$$\text{ATTD N}_{\text{FRCP}}[\%] = \frac{\begin{array}{c}(\text{diet}_{\text{DM}}[\text{g/d}] \times \text{diet}_{\text{N}}[\%]\text{- (fecal}_{\text{DM}}[\text{g/d}] \\ \times\ \text{fecal}_{\text{N}}[\%]\text{-}BD_{\text{DM}}[\text{g/d}] \times \text{BD}_{\text{N}}[\%]) \\ \times\ (1\text{-(ATTD}_{\text{N \_ BD}}/100)))\end{array}}{\text{diet}_{\text{DM}}[\text{g/d}] \times \text{diet}_{\text{N}}[\%]} \times 100.$$

Energy in urine was calculated from the urine N content:

$$\text{Urine GE output } [\text{MJ/d}] = \frac{\text{Urine N}\,[\text{g/d}] \times 50.41\,[\text{kJ/g}]}{1{,}000\ [\text{kJ/MJ}]}.$$

Assuming that urine from sows contained 50.41 kJ/g N (Theil et al. 2002, 2004)

'Heat production' (**HP**) was calculated indirectly, as the difference between metabolizable energy and total energy retained, using the C and N balance (CN method). Where the C balance gives the total amount of retained C in the body and the N balance the protein (N × 6.25) retained, assuming that all energy retained is either fat or protein (Brouwer 1965). Energy in fat was calculated by subtracting retained C in protein (assuming protein contains 16% N, 52% C, and 23.86 kJ/g) from the total C method (assuming that fat contains 76.7% C and 39.76 kJ/g; Brouwer, 1965). Retained energy as protein was calculated as follows:

$$\text{Retained energy}_{\text{protein}}\ [\text{kJ}] = \&\text{Retained N}\,[\text{g}] \times 6.25 \times 23.86\,[\text{kJ/g}]\,,$$

and retained energy as fat as:

$$\text{Retained energy}_{\text{fat}}\,[\text{kJ}] = (\text{Retained C}\,[\text{g}] - \text{Retained N}\,[\text{g}] \times 6.25 \times 0.52) \times \frac{1}{0.767} \times 39.76\,[\text{kJ/g}]\,.$$

Then the HP was calculated:

$$\text{HP}\,[\text{kJ}] = \text{ME}\,[\text{kJ}] - (\text{Retained energy}_{\text{protein}}\ [\text{kJ}] + \text{Retained energy}_{\text{fat}}\,[\text{kJ}])\,,$$

and the HP divided into nonactivity related HP and activity related HP was calculated according to Brouwer (1965), except that energy from urine was not included:

$$\text{daily HP}\,[\text{kJ}] = 16.181 \times O_2\,[L] + 5.023 \times CO_2\,[L] - 2.168 \times CH_4\,[L]\,.$$

Assuming that 1 kcal = 4.1855 kJ.

The nonactivity related HP was defined as the HP between 2100 and 0500 hours (Figure 1), while the activity related HP was calculated by subtracting the daily nonactivity related HP from the daily HP.

'Statistical analyses' were performed using the following model:

$$Y_{ijk} = \mu + \alpha_i + \delta_j + \tau_k + \varepsilon_{ijk},$$

where Y_{ijk} is the response variable, μ is the overall mean, α_i is the fixed effect of treatment (i = BD, BG, PH, PR, PP, SR, or SBP), δ_j is the random effect of sow (j = 1, 2, 3…, 8), τ_k is the random effect of block (k = 1, 2, or 3), and ε_{ijk} is the residual error component, which was assumed to be normally distributed N (0, σ^2).

The data were analyzed using the mixed model in the SAS software (version 9.4, SAS Institute Inc., Cary, NC, 2012). The results are presented as means ± standard error of means (SEM), and the highest SEM are shown. A probability value of $P \leq 0.05$ was considered significant, and a tendencies when $0.05 < P \leq 0.10$.

Results

Chemical composition of fiber-rich components and diets

Two of the six FRCP (SR and PH) were dry with a DM content of 92.1% and 90.2%, respectively (Table 1), whereas the other coproducts, BSG, PP, PR, and SBP, were wet, with DM contents ranging between 17.5% and 24.2%. The CP content was greatest in the BSG FRCP with 23.1% while the CP content of BD, SBP, SR and PR, was between 6.4% and 13.6%, and with the lowest CP content in the PP FRCP with 5.5%. Total NSP content in the FRCP ranged from 45.0% (BSG) to 73.3% (PR), while the lignin content ranged from 0.9% in the PH to 12.9 in the BSG FRCP.

The inclusion levels of the dry FRCP were higher absolute and relative (2,235 to 2,319 g DM/d; 61.8% to 63.0%), than of the wet supplements (1,576 to 1,967 g DM/d; 46.3% to 58.5%; Table 2). There was a strong correlation between the calculated total fiber (cTF) and analyzed total fiber (r = 0.979, $P < 0.001$). The cTF content was highest in the PR

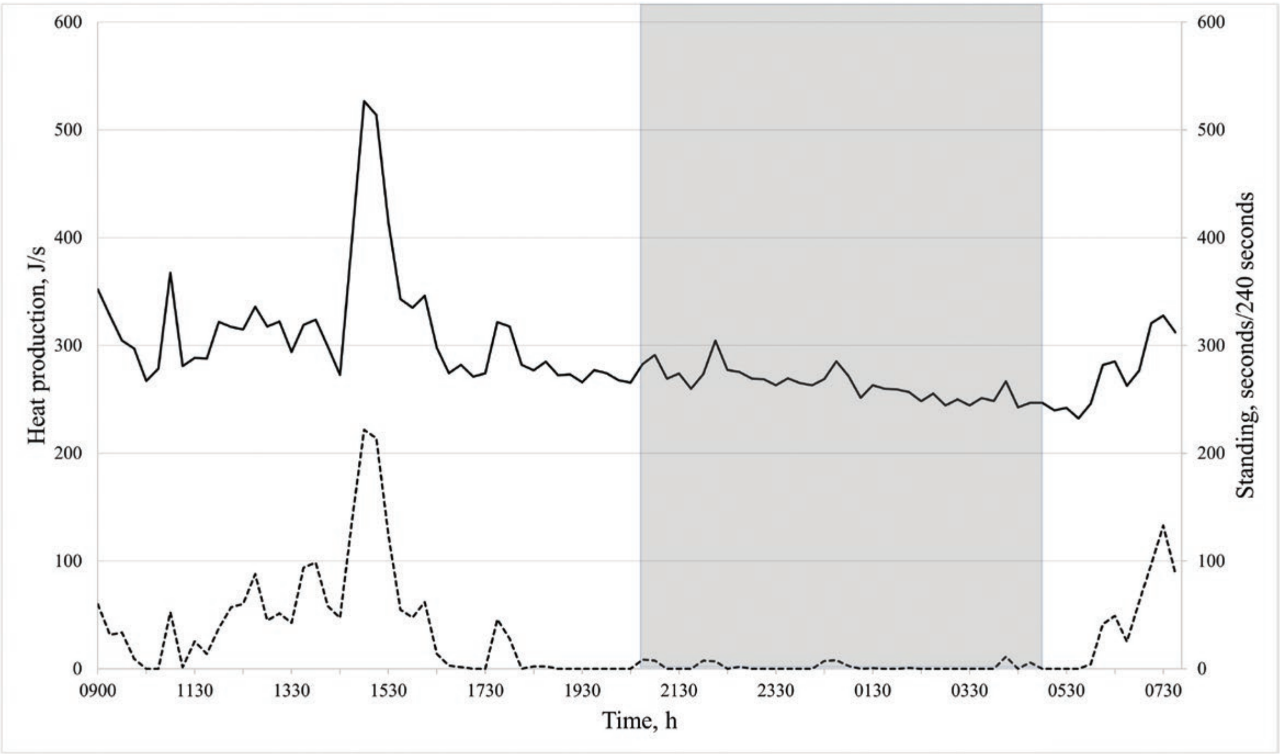


Figure 1. Typically daily distribution of heat production (HP; solid line) and seconds out of 240 s spend standing (dotted line). The gray area is the timeframe that defines (2100 to 0500 hours) the nonactivity related HP.

Table 1. Analyzed chemical composition (% DM) of the basal diet and fiber-rich coproducts (FRCP)

		FRCP[1]					
Item[2]	BD[3]	SR	BSG	PH	PP	PR	SBP
Chemical composition, % DM							
Dry matter	88.7	92.1	24.2	90.2	17.5	18.7	21.2
Ash	4.9	8.8	4.3	3.0	3.9	1.5	5.6
Crude protein (N×6.25)	13.6	9.0	23.1	13.2	5.5	6.4	9.7
Fat	5.1	2.4	11.3	2.1	0.4	4.6	2.4
Crude fiber	4.6	29.5	16.7	39.5	21.0	48.4	21.9
Nitrogen free extract	72.0	50.8	45.2	41.8	69.5	39.1	60.5
Sugar	3.8	5.6	0.2	3.6	0.1	0.2	3.8
Starch	51.5	9.4	5.9	14.6	27.0	0.7	0.3
S-NCP	5.2	4.8	2.2	10.5	24.7	14.6	30.2
I-NCP	8.0	21.3	28.6	13.6	13.7	20.0	21.1
Cellulose	3.6	25.3	14.2	35.7	23.0	38.6	21.8
Total NSP	16.7	51.4	45.0	59.8	61.4	73.3	73.1
Klason lignin	3.1	12.5	12.9	0.9	2.4	10.8	2.7
Total fiber	19.8	63.9	57.9	60.6	63.8	84.0	75.7
cTF[4]	21.1	64.7	55.2	63.6	63.1	86.1	78.3
Gross energy, MJ/kg	18.59	18.29	21.47	18.01	16.97	18.83	17.35
EFOS	87.0	33.3	48.7	73.9	74.1	69.0	90.2

[1] SR, seed residue; BSG, brewers spent grain; PP, potato pulp; PH, pea hull; PR, pectin residue; SBP, sugar beet pulp.
[2] cTF, calculated total fiber; EFOS, in vitro enzyme digestible organic matter; I-NCP, insoluble non-cellulose polysaccharides; NSP, nonstarch polysaccharides; S-NSP, Soluble noncellulose polysaccharides.
[3] Ingredients (as is) in the basal diet (BD): Barley (856 g/kg), soya bean meal (80 g/kg), animal fat (20 g/kg), sugar beet molasses (20 g/kg), calcium carbonate (14 g/kg), mono calcium phosphate (5 g/kg), sodium chloride (3 g/kg), vitamin micromin. Mix (2 g/kg).
[4] cTF = 100 − (ash + protein + fat + starch + sugar) (Noel et al., 2022).

Table 2. Chemical composition (% of DM) of the diets including the fiber-rich coproducts

	Diet[1]					
	SR	BSG	PH	PP	PR	SBP
Chemical composition[2], % DM						
Dry matter	90.8	34.7	89.6	30.7	32.5	35.8
Ash	7.3	4.6	3.7	4.4	3.3	5.2
Organic matter	92.7	95.4	96.3	95.6	96.7	94.8
Crude protein (N × 6.25)	10.8	19.2	13.4	9.9	10.3	11.8
Fat	3.5	8.7	3.2	2.9	4.8	3.8
Crude fiber	20.0	11.7	26.6	12.2	24.9	12.8
Nitrogen-free extract	58.5	55.9	53.2	70.6	56.7	66.4
Sugar	4.9	1.7	3.7	2.1	2.1	3.8
Starch	25.5	24.8	28.3	40.1	27.9	27.3
S-NCP	5.0	3.4	8.5	14.3	9.6	17.0
I-NCP	16.2	20.0	11.5	10.6	13.6	14.2
Cellulose	17.0	9.8	23.8	12.6	19.8	12.2
NSP	38.2	33.2	43.8	37.5	42.9	43.3
Klason lignin	8.9	8.8	1.7	2.8	6.7	2.9
Total fiber	47.1	42.1	45.5	40.2	49.5	46.2
cTF[3]	49.5	42.6	49.2	42.6	53.5	50.1
Gross energy, MJ/kg	18.4	20.3	18.2	17.8	18.7	18.0
EFOS	53.8	64.6	78.7	81.0	78.7	88.5

[1] SR, seed residue; BSG, brewers spent grain; PH, pea hull; PP, potato pulp; PR, pectin residue; SBP, sugar beet pulp.
[2] cTF, calculated total fiber; EFOS, in vitro enzyme digestible organic matter; I-NCP, insoluble noncellulosic polysaccharides; NSP, nonstarch polysaccharides; S-NSP, Soluble noncellulosic polysaccharides.
[3] cTF = 100 − (ash + protein + fat + starch + sugar) (Noel, et al. 2022).

diet (53.5%) followed by the SBP, SR, PH, BSG, and PP diets (50.1%, 49.5%, 49.2%, 42.6%, and 42.6%), respectively. The CP content ranged from 9.9% to 19.2% and fat from 2.9% to 8.7%. The GE content was greatest in the BSG diet (20.27 MJ/kg), whereas the other FRCP diets ranged from 17.84 MJ/kg in the PP diet to 18.70 MJ/kg in the PR diet.

Digestibility of diets and fiber-rich components

The ATTDs of GE, DM, and OM were almost similar for the BD, PP, and SBP diets, whereas these parameters, in general, were lower for the SR, BSG, PH, and PR diets (Table 3). The ATTD of N was greatest, in BD, PH, and SBP fed sows (83%, 76%, and 71%, respectively) and lowest in SR and PR fed sows [47% and 57%, respectively ($P < 0.01$)]. The ATTD of cTF was greater in the PP and SBP diets (87% to 88%) than the other FRCP diets (14% to 76%) as well as the BD (66%; $P < 0.001$).

The ATTD of DM, OM, cTF, and GE were highest for PP, PH, and SBP FRCPs, which ranged between 81% to 86%, 85% to 87%, 86% to 91%, and 79% to 83%, respectively ($P < 0.001$). The ATTD of N ranged from −9% to 72%, being highest and lowest for the PR and PH FRCPs, respectively. The SR FRCP had the lowest ATTD of all nutrients ($P < 0.001$) followed by the PR, which was intermediate in ATTD of all nutrients. Both digestible and metabolizable energy were greatest for PH, PP, and SBP, intermediate for BSG and PR and lowest for SR FRCPs.

Nitrogen and carbon utilization

For the diets, the realized N intake and urine N output was greatest in BSG fed sows and fecal N output was highest for BSG and SR fed sows ($P < 0.001$; Table 4). The PP and PR diets resulted in the lowest N intake followed by the SBP diet. Total N retention, however, did not differ among treatments. The urine N output was higher than the fecal N output in all diets except for the SR diet. In the SR fed sows, the fecal N output accounted for 55% of total N intake, while it was between 19% (BD) and 42% (PR) for the remaining diets.

The C intake was greatest and on average, 999 g/d for BSG, SR, and PH fed sows while it was lower and on average 736 g/d following the BD, PP, PR, and SBP diets ($P < 0.001$). The fecal C output was lowest (108 to 120 g/d) for BD, PP, and SBP fed sows, intermediate (176 to 238 g/d) for PH and PR fed sows and highest (349 to 556 g/d) for BSG and SR fed sows ($P < 0.001$). The urine C output was much less than the fecal; from 24.6 g/d in SR fed sows to 36.5 g/d in BSG fed sows ($P < 0.05$), whereas the CO_2C output only differed for PH fed sows relative to sows fed the other diets ($P < 0.001$). The total C retention was lowest with mobilization of 118.4 g C/d in SR fed sows and greatest, with retention of 147.2 g/d in the PH fed sows ($P < 0.001$).

Energy metabolism and utilization

The GE intake ranged between 28.5 and 42.3 MJ/d and it was greatest in PH, SR, and BSG fed sows ($P < 0.001$; Table 5). The fecal GE output was high (22.9 MJ/d, $P < 0.001$) in SR fed sows, followed by sows fed BSG and PR and the remaining diets resulted in fecal GE outputs of 4.7 to 7.6 MJ/d. The HP did not differ among treatments ($P = 0.68$); however, the nonactivity related HP was higher for PH and SBP fed sows and lowest in SR and BD fed sows. In contrast, SR fed sows had the highest and the PH and SBP the lowest activity related

Table 3. Total tract digestibility (ATTD) of nutrients and energy in diets and fiber-rich coproducts (FRCP) fed to sows

	Basal diet	FRCP[1]							
		SR	BSG	PH	PP	PR	SBP	SEM	*P*-value
N	7	4	5	4	5	6	5		
Inclusion of FRCP, % of Dry matter (DM)		61.8	58.5	63.0	46.4	46.3	47.1		
DM intake, g/d	1,720	2,240	1,965	2,324	1,597	1,588	1636		
Apparent total tract digestibility of diets, %									
DM	84^{a}	43^{c}	63^{b}	83^{a}	86^{a}	70^{b}	84^{a}	4	<0.001
Organic matter	87^{a}	47^{c}	65^{b}	85^{a}	87^{a}	71^{b}	87^{a}	4	<0.001
Nitrogen	83^{a}	47^{d}	70^{b}	76^{a}	$62^{b,c}$	$57^{c,d}$	$71^{a,b}$	5	<0.01
Fat	65^{a}	28^{c}	$55^{a,b}$	$51^{a,b}$	$38^{b,c}$	$46^{a,b,c}$	$42^{b,c}$	7	<0.001
Calculated total fiber (cTF)	66^{b}	14^{d}	41^{c}	$76^{a,b}$	87^{a}	64^{b}	88^{a}	6	<0.001
Gross energy	84^{a}	44^{c}	63^{b}	82^{a}	83^{a}	67^{b}	83^{a}	4	<0.001
Apparent total tract digestibility of FRCP, %									
Dry matter		21^{c}	49^{b}	85^{a}	86^{a}	49^{b}	81^{a}	4	<0.001
Organic matter		24^{c}	51^{b}	86^{a}	87^{a}	51^{b}	85^{a}	4	<0.001
N		14^{b}	66^{a}	72^{a}	17^{b}	-9^{b}	53^{a}	11	<0.001
Fat		–[2]	55^{a}	–[2]	–[2]	17^{b}	–[2]	6	<0.01
cTF		9^{d}	38^{c}	86^{a}	91^{a}	57^{b}	91^{a}	5	<0.001
Gross energy		22^{c}	51^{b}	83^{a}	81^{a}	44^{b}	79^{a}	5	<0.001
Digestible and metabolizable energy of FRCP, MJ × $kgDM^{-1}$									
Digestible energy		4.0^{c}	11.0^{b}	15.0^{a}	13.8^{a}	8.3^{c}	13.7^{a}	0.9	<0.001
Metabolizable energy		3.9^{c}	10.0^{b}	14.5^{a}	13.8^{a}	8.3^{b}	13.4^{a}	0.8	<0.001

[1] SR, seed residue (dry); BSG, brewers spent grain (wet); PH, pea hull (dry); PP, potato pulp (wet); PR, pectin residue (wet); SBP, sugar beet pulp (wet).

[2] Not included, due to a low intake of fat.

[a,b,c,d] Means within a row with different superscripts differ ($P < 0.05$).

Table 4. Dry matter intake and utilization of Nitrogen (N) and carbon (C) in sows

	Diet[1]								
	BD	SR	BSG	PH	PP	PR	SBP	SEM	*P*-value
n	7	4	5	4	5	6	5		
Nitrogen utilization, g/d									
Nitrogen intake	37.3^{c}	38.6^{c}	60.3^{a}	49.6^{b}	25.1^{e}	26.0^{e}	30.6^{d}	1.4	<0.001
Fecal N output	7.0^{c}	21.2^{a}	18.1^{a}	12.4^{b}	$9.3^{b,c}$	$11.0^{b,c}$	$8.9^{b,c}$	1.7	<0.001
Urine N output	24.1^{b}	14.0^{b}	40.0^{a}	24.6^{b}	18.4^{b}	15.6^{b}	20.9^{b}	4.9	<0.001
Total N retention[2]	5.8	3.1	1.3	11.3	−1.7	0.4	1.7	4.7	0.2
Carbon utilization, g/d									
Carbon intake	769^{b}	1008^{a}	946^{a}	1044^{a}	707^{b}	736^{b}	733^{b}	36	<0.001
Fecal C output	120^{d}	556^{a}	349^{b}	$176^{c,d}$	108^{d}	238^{c}	118^{d}	34	<0.001
Urine C output	$31.3^{a,b,c}$	24.6^{c}	36.5^{a}	$32.7^{a,b}$	$27.6^{b,c}$	$25.8^{b,c}$	$31.2^{a,b,c}$	2.6	<0.05
Carbon dioxide C output	573^{b}	537^{b}	568^{b}	668^{a}	576^{b}	559^{b}	586^{b}	19	<0.001
Methane C output	3.5^{c}	4.21^{c}	4.7^{c}	15.1^{a}	8.7^{b}	2.4^{c}	8.0^{b}	0.8	<0.001
Total C retention[2]	$44.2^{a,b}$	-118.4^{c}	$-12.9^{b,c}$	147.2^{a}	$-4.9^{b,c}$	$-82.0^{b,c}$	$-10.4^{b,c}$	45.8	<0.001

[1] BD, basal diet; SR, seed residue (dry); BSG, brewers spent grain (wet); PH, pea hull (dry); PP, potato pulp (wet); PR, pectin residue (wet); SBP, sugar beet pulp (wet).

[2] Positive values are retention, while negative values are mobilization.

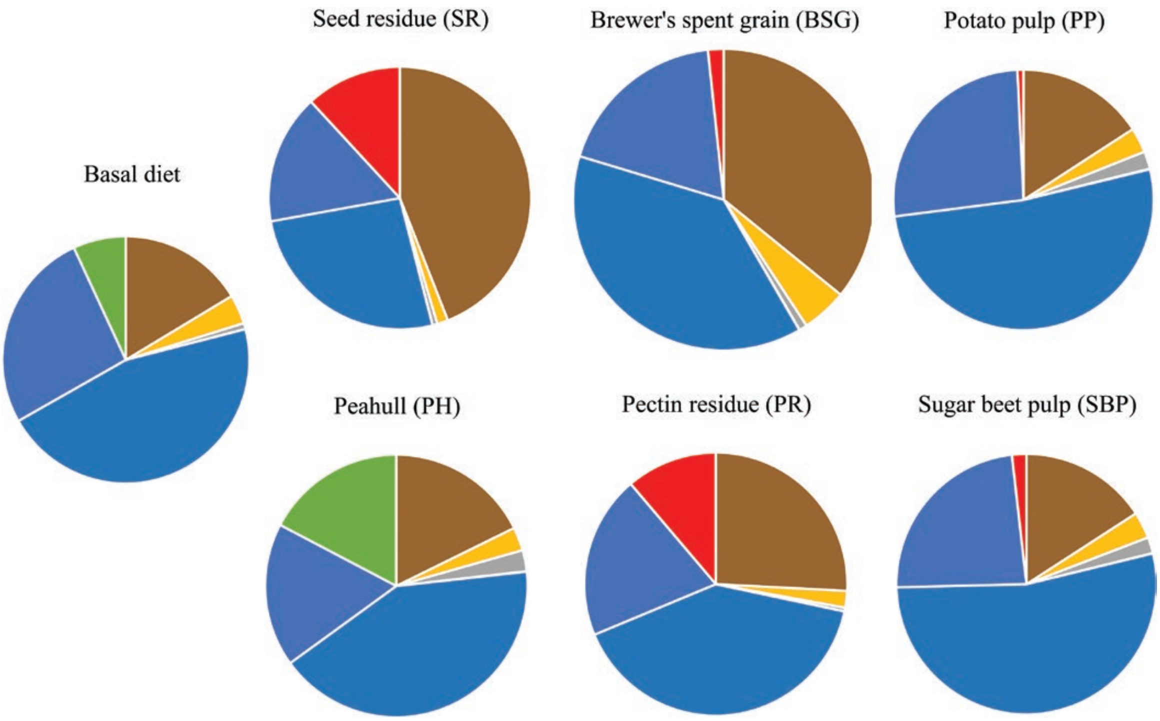
[a,b,c,d] Means within a row with different superscripts differ ($P < 0.05$).

HP ($P < 0.05$). Overall, HP accounted for most of GE output (Figure 2), with an output between 57% and 80% of intake, in SR and PP fed sows, respectively. Total energy retention was greatest in PH fed sows (7.42 MJ/d), followed by BD fed sows (2.19 MJ/d), intermediate for SBP, PP, and BSG fed sows, who retained 0.57 MJ/d and mobilized 0.22 and 0.69 MJ/d, respectively, and lowest in PR and SR fed sows, who mobilized 4.26 and 6.17 MJ/d, respectively ($P < 0.001$).

Table 5. Energy metabolism of sows fed the experimental diets

	Diet[1]								
	BD	SR	BSG	PH	PP	PR	SBP	SEM	*P*-value
n	7	4	5	4	5	6	5		
Sow body weight, kg	205	210	207	219	211	209	210		
Energy utilization									
Gross energy (GE) intake, MJ/d	31.9^{b}	41.2^{a}	39.8^{a}	42.3^{a}	28.5^{c}	29.7^{b,c}	29.4^{b,c}	1.0	<0.001
Fecal GE output, MJ/d	5.2^{c}	22.9^{a}	14.8^{b}	7.6^{b,c}	4.7^{c}	9.8^{b}	5.0^{c}	1.4	<0.001
Urine GE output[2], MJ/d	1.22^{b}	0.71^{b}	2.02^{a}	1.24^{b}	0.93^{b}	0.78^{b}	1.05^{b}	0.25	<0.001
Methane GE output, MJ/d	0.24^{c}	0.31^{c}	0.35^{c}	1.11^{a}	0.65^{b}	0.17^{c}	0.63^{b}	0.07	<0.001
Hydrogen GE output, MJ/d	0.006	0.007	0.014	0.020	0.018	0.007	0.010	0.006	0.38
Metabolizable energy (ME), MJ/d	25.3^{b}	17.3^{c}	22.7^{b}	32.4^{a}	22.2^{b,c}	18.8^{c}	22.8^{b}	1.7	<0.001
Metabolizability (ME:GE), %	79.5^{a}	42.6^{c}	57.3^{b}	77.1^{a}	77.3^{a}	63.0^{b}	76.8^{a}	3.5	<0.001
Heat production (HP), MJ/d	23.3	23.4	23.4	24.8	22.7	23.4	23.2	1.2	0.68
Nonactivity-related HP, MJ/d	18.1^{c}	17.0^{c}	19.6^{a,b,c}	22.4^{a}	19.2^{b,c}	19.2^{b,c}	21.2^{a,b}	1.0	<0.001
Activity-related HP, MJ/d	4.7^{a,b}	5.0^{a}	3.8^{a,b}	3.2^{b}	3.9^{a,b}	3.8^{a,b}	3.2^{b}	0.5	<0.05
Total energy retention, MJ/d	2.19^{a,b}	−6.17^{c}	−0.69^{b,c}	7.42^{a}	−0.22^{b,c}	−4.26^{b,c}	0.57^{b,c}	2.34	<0.001
Retained energy as fat[3], MJ/d	1.35^{a,b}	−6.51^{c}	−0.93^{a,b,c}	5.72^{a}	−0.05^{a,b,c}	−4.28^{b,c}	−0.80^{a,b,c}	2.22	<0.001
Retained energy as protein[3], MJ/d	0.86	0.31	0.20	1.68	-0.25	0.06	0.25	0.70	0.16
Standing activity, min/d	303	371	318	248	249	256	326	53	0.24

[1] BD, basal diet; SR, seed residue (dry); BSG, brewers spent grain (wet); PH, pea hull (dry); PP, potato pulp (wet); PR, pectin residue (wet); SBP, sugar beet pulp (wet).
[2] Assuming that energy in urine from sows contains 50.41 kJ/g N (Theil et al. 2002, 2004).
[3] Positive values are retention, while negative values are mobilization.
[a,b,c,d] Means within a row with different superscripts differ ($P < 0.05$).



Seed residue (SR)

Brewer's spent grain (BSG)

Potato pulp (PP)

Basal diet

Peahull (PH)

Pectin residue (PR)

Sugar beet pulp (SBP)

Figure 2. Distribution of gross energy (GE) utilization in sows, fecal GE output (brown), urine GE output (yellow), methane GE output (light gray) hydrogen GE output (dark gray), nonactivity related heat production (HP; dark blue) activity related HP (light blue), retained energy (green) and mobilized energy (red).

Discussion

Fiber sources and digestibility

The FRCP were all relatively high in total fiber and not different from what has been described earlier following an investigation of the variation in chemical composition and physicochemical properties of similar FRCPs (Serena and Bach Knudsen, 2007). In the current study, we used the FRCP in the form they were provided from the industry (wet or dry), and we intended to include the different FRCP in the diet at around 60% of the DM intake. In peak lactation, high prolific sows are fed around

9 kg/d of feed, equivalent to around 2 kg/d of cTF, which is significantly higher than following all treatments in the current study. However, the dry and gestating sow does not need as much energy as in lactation, and furthermore, in early and midgestation the gut volume is not limited by large fetuses. The amount of FRCP that could be consumed by the sows, was highest for the FRCP with the lowest content of S-NCP (SR, BSG, and PH) and lowest for the FRCP with the highest content of S-NCP (PP, PR, and SBP). This corroborated findings of Serena and Bach Knudsen (2007), who found that PP, PR, and SBP were the FRCPs with the highest swelling capacity. It is likely, that the higher swelling capacity of these FRCP rather than the ATTD of nutrients, is the factor largely influencing the amount of FRCP that can be incorporated into the diet (Serena and Bach Knudsen, 2007). A high swelling capacity together with a low lignin content enables a larger surface area, which allows the bacteria of the large intestine to degrade the fiber matrix more efficiently. On the contrary, a high lignin content will cross-link the polysaccharides of the NSP fraction, thereby decreasing the ATTD of cTF and of nutrients in general (Bach Knudsen, 2001; Noblet and Le Goff, 2001). The FRCP PP, SBP, and PH were all found to have similar ATTD of DM, OM, and GE as the BD. However, the ATTD of cTF of the FRCP PP, SBP, and PH was higher than of BD (73% to 83% vs. 66%) whereas the ATTD of N was lower than of BD (17% to 72% vs. 83%). When provided in the diets, however, PH and SBP diets had similar ATTD of N as the BD, which agrees with Wisbech et al. (2022), when taking the greater inclusion of FRCP in the current study into account. It is also aligns with Serena et al. (2008b), who found no difference between ATTD of N in a high-fiber diet containing a mix of PP, PR, and SBP compared to a control diet based on barley, wheat, and soybean meal as the main ingredients. These results indicate that SBP and PH have the potential to largely replace cereal grains in the diet of gestating sows.

Of the studied FRCP, the highest lignin content was found in the SR, BSG, and PR, which also were the FRCPs with the lowest digestible and metabolizable energy content. This agrees with Serena and Bach Knudsen (2007), who found that maintaining bodyweight was compromised when a diet containing 420 g TF/kg DM from FRCPs containing mainly insoluble fibers (SR, BSG, and PH) replaced wheat and barley. The same replacement by FRCP sources containing mainly soluble fiber (PP, PR, SBP) did not compromise body weight.

The sows have the capacity to handle large quantities of TF in their digestive system between weaning and the last part of the gestation period. In comparison, growing-finishing pigs have a shorter gastrointestinal tract and lower fermentative capacity of the large intestine than sows, resulting in lower ATTD of N, fat, and cTF of all the FRCPs used in the current study (Serena et al., 2007).

Energy utilization

The intake of GE was higher for SR, BSG, and PH than for PP, PR, and SBP fed sows but when it comes to how the energy is digested and utilized, the picture is somewhat different. Thus, the SR, BSG, and PH fed sows all had almost similar and highest GE intake but at the same time the lowest (SR), intermediate (BSG), and highest (PH) energy retention. This is due to differences in the sows ability to digest and utilize the energy; SR fed sows showed the lowest energy digestibility, BSG fed sows intermediate energy digestibility but a high urine energy excretion, and PH fed sows a high energy digestibility, a low urinary energy excretion, and the highest energy retention as fat; the latter considered favorable in sows (Wisbech et al., 2022). The high urinary energy excretion when consuming the BSG diet is due to the N content being twice as high as recommended (Tybirk et al., 2020). The N intake and urine N output in BSG fed sows, aligns with previous findings (Le Goff and Noblet, 2001), whereas the fecal N output was higher than found by Le Goff and Noblet (2001). For PP, PR, and SBP the GE intake was lower than that of the other diets. However, the energy digestibility was still high for PP and SBP but lower for PR, the latter also having the lowest methane GE output of all diets. SBP is a well-recognized FRCP for sows (Jha and Berrocoso, 2015) and a comparison of PP and PH with SBP in our study indicate that PP and PH are having some of the same digestion and metabolism properties as SBP. In the current study, the metabolizable energy value for SBP was found to be slightly lower compared to results by Wisbech et al. (2022), who found a metabolizable energy value for SBP around 14.2 MJ/kg (as-is basis), independent of inclusion level up to 210 g SBP/kg supplemented to a wheat/barley diet. Serena et al. (2008b) also showed that the metabolizable energy value of a low fiber diet and a diet high in soluble fiber (PP, PR, and SBP) was comparable to the metabolizable energy values of PH, PP, and SBP in the current study.

Total energy retention is highly depended on how much of the energy is spent on HP. In the current study, 57% to 80% of GE intake was lost as heat, which is in line with previous studies (Müller and Kirchgeßner, 1998; Theil et al., 2002; Wisbech et al., 2022). In contrast to results by Ramonet et al (2000), the total HP did, however, not differ among treatments. Ramonet et al (2000) reported that sows fed with a high-fiber diet had a greater total HP than sows fed with a low fiber diet, but with no activity related differences between the two treatments. On the other hand, Rijnen et al. (2003) observed a decrease in activity related HP with increasing SBP levels. This is in line with the current results showing that activity related HP differed among treatments being highest in SR fed sows and lowest in PH and SBP fed sows. Our findings also align with Jørgensen et al. (2010), who found that activity related HP was lower when sows were fed a diet high in S-NCP compared to sows fed a diet high in I-NCP. In the current study, the PP and SBP diets had the highest S-NCP content, and SBP fed sows the greatest total S-NCP intake followed by the PH and PP fed sows. This could indicate that it is the daily intake of S-NCP, rather than solely the S-NCP content that influences the activity related HP.

Conclusion

This study confirmed our hypothesis, that the ATTD of nutrients and energy differed between the studied FRCP according to NSP composition and degree of lignification. The relatively high ATTD of all nutrients of SBP and PH makes them ideal suited to partly substitute high-value grains in sow feed. In contrast, SR and PR show relatively low ATTD of all nutrients, which mainly makes them suited as gut fill with low nutritional value. PP and BSG were found to compromise the N utilization giving rise to high fecal N and urine N outputs, respectively.

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Conflict of Interest Statement

The authors declare no real or perceived conflicts of interest.

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SECTION 6. GENERAL DISCUSSION

In this PhD thesis, energy and nutrient digestibility and utilization of diets containing increasing levels of fiber and different fiber-rich co-products were investigated.

6.1. Fiber-rich co-products as feed ingredients for sows

The fiber-rich co-products chosen in the studies included in the current thesis were all relatively high in TF but differed in composition both between and within the co-product. The fiber level in the diets (percent of DM) was around twice as high in experiment II (Paper III) compared to experiment I (Papers I and II), see Figure 6.1.1.

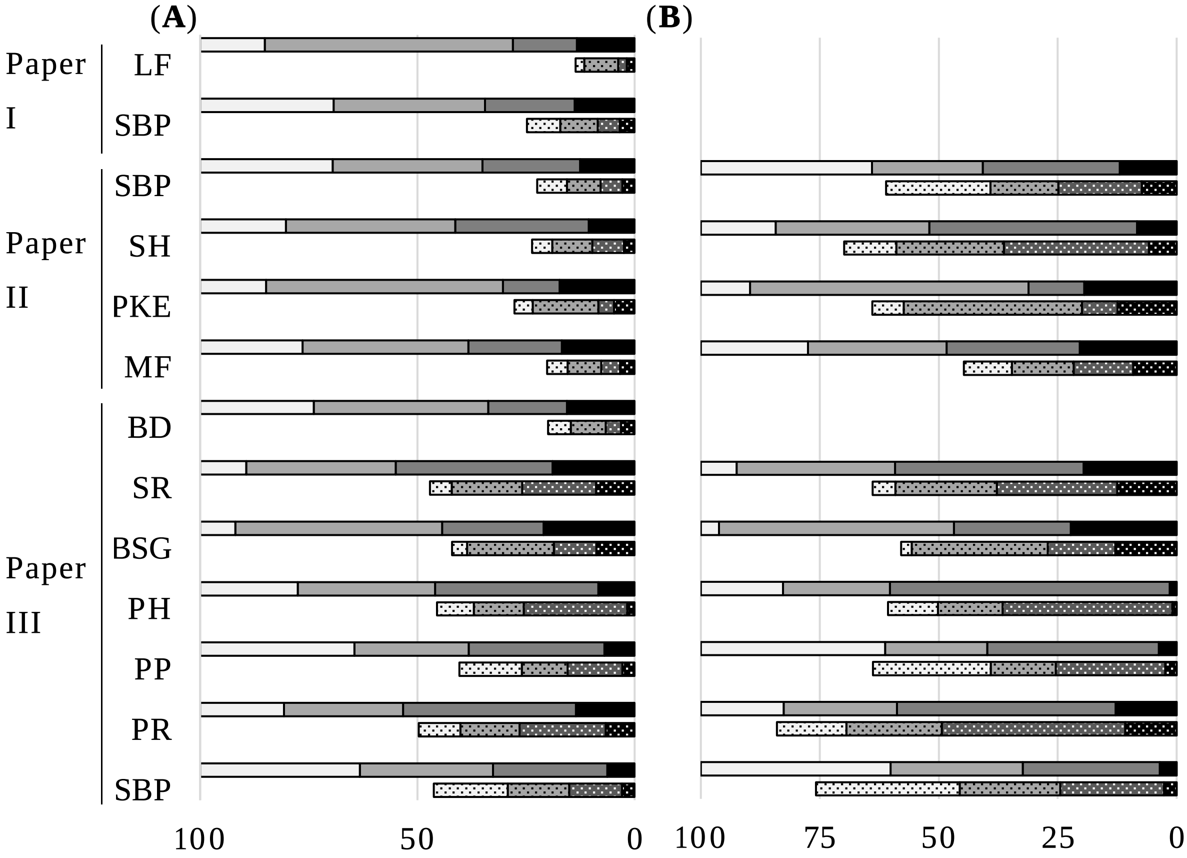

Figure 6.1.1 - Fiber composition of the diets (**A**) and fiber-rich supplements (**B**), decreasing in fermentability from left to right; soluble non-starch polysaccharides (white), insoluble non-cellulosic polysaccharides (light grey), cellulose (dark grey) and lignin (black) content, % of total fiber (TF) (solid) and % of DM (with dots) of the experimental diets: LF, low fiber (based on wheat and barley); SBP, sugar beet pulp; SH, soy hull; PKE, palm kernel expellers; MF, mixed fiber (SBP, oat hulls, wood fibers and yeast); BD, basal diet (based on barley) SR, seed residue; BSG, brewers spent grain; PH, pea hull; PP, potato pulp; PR, pectin residue).

The only fiber-rich co-product included in all three papers was sugar beet pulp which also differed in composition between the two experiments with lignin representing 13.8 and 12.6 % of TF in papers I and II, respectively, compared to 6.0 % of TF in paper III. A reason for the difference between the two experiments could be that the sugar beet pulp in experiment 2 was provided in wet form and freeze-dried before being analyzed whereas in experiment 1 the sugar beet pulp was provided in dry form. It can't be excluded that the drying process had resulted in the formation of a fraction that is acid insoluble and therefore measured as lignin (Theander, 1983). Among the diets, potato pulp had the lowest lignin content whereas seed residue and brewers spent grain had the highest, followed by pectin residue and palm kernel expellers. In paper III, pea hull and sugar beet pulp had the highest proportion of soluble NSP (**S-NSP**) followed by sugar beet pulp in paper I and II. Regarding content of S-NSP, it was highest in pea hull and sugar beet pulp in paper III, followed by pectin residue and potato pulp, both having a slightly higher S-NSP content than sugar beet pulp in papers I and II.

The fiber-rich co-products used in paper III were the same as those studied by Serena and Knudsen (2007), where the co-products were collected from the same producer and analyzed four times each season for two consecutive seasons. All fiber-rich co-products had a greater standard deviation of total NSP ranging from 27 to 58 g/kg DM compared to wheat and barley, which had a standard deviation of 8 and 13, respectively. However, compared to paper III all co-products used, except pea hull, were within the 95% confidence interval of NSP found by Serena and Knudsen (2007), and all within the interval regarding lignin. Regarding sugar beet pulp, the product used in paper II was almost three times higher in lignin content than sugar beet pulp that used in paper III, and above the 95% confidence interval of what was reported by Serena and Bach Knudsen. On the contrary, the NSP content of sugar beet pulp in paper II was below the 95 % confidence interval with a NSP content of 538 g/kg DM, compared to 700 g/kg DM and standard deviation of 27 g/kg DM found by Serena and Bach Knudsen. The latter was in line with the 733 g NSP/kg DM found in sugar beet pulp in paper III. Compared to data in the literature the lignin content in the sugar beet pulp used in paper II was high (Bach Knudsen, 1997; Fadel et al., 2000; Navarro et al., 2018). In another study with distillers dried grain with solubles from 24 different producers, it was found that the distillers dried grain with solubles had a large variability in the NSP profile with a standard deviation up to 20 g/kg DM (Pedersen et al., 2014) influenced by the producer and by the type of raw materials used; maize, wheat or mixed grains. In this respect, the brewers spent grain used in paper III differed from the distillers dried grain with soluble from maize, wheat or mixed product by being based mainly on barley.

It was not only the content and proportion of fiber that differ in different fiber-rich co-products but also that of other nutrients such as CP. Crude protein was greater, 143 and 190%, respectively, for brewers spent grain (paper III) and palm kernel expellers (paper II) compared with barley (Serena and Knudsen, 2007). In the study of Serena and Knudsen (2007) the standard deviation for CP content in the co-products were up to four fold higher than of cereals.

When focusing on the utilization (to be discussed later) the protein to energy ratio, but also each AA to protein and between AA (the profile), is of importance. This is especially the case for the lysine to protein ratio, as lysine is the first limiting AA in swine diets. These ratios are important to have in mind when using the fiber-rich co-products in sow diets, since a high protein to energy ratio and imbalanced AA profile reduce feed efficiency (Pedersen et al., 2018). Of the fiber-rich co-products, both palm kernel expellers and brewers spent grain stands out compared to the other co-products because of their high protein content, but not in energy and lysine content, resulting in a high protein to energy ratio and low lysine to CP ratio. Furthermore the imbalanced AA profile of the palm kernel expellers could also, due to a high arginine content, impair uptake of lysine (Stein et al., 2015).

However, in a balanced diet this should not be of great importance. Processing can cause formation of Maillard products, which can damage the AA (Oliveira et al., 2021). The Maillard process is a well-known reaction in the oil extraction process (Son et al., 2014), e.g. when producing palm oil with palm kernel expellers as a co-product, or in the malt processing when making beer with brewers spent grain as a co-product (Farcas et al., 2021). A conventional AA analysis of the fiber-rich co-product will reveal the AA content but not the degree of potential damage to the protein/AA, which can make it difficult to correctly formulate the diet, as it may be deficient in digestible AA (Oliveira et al., 2021).

6.2. Apparent total tract digestibility when fiber-rich co-products are included in diets fed to sows

When the sows were fed diets containing sugar beet pulp, the ATTD did not seem to differ much for DM and organic matter (**OM**), Table 6.2.1. The ATTD of NSP increased with increasing fiber inclusion (paper I). Apparent total tract digestibility of GE and N were lower in paper III compared to papers I and II.

Comparing the fiber rich co-products, the ATTD of DM, OM and GE was similar for sugar beet pulp, soy hull, palm kernel expellers, mixed fiber, pea hull and potato pulp, while ATTD of N were lower for potato pulp compared to the above mentioned. The ATTD of all nutrients and energy was lowest in the seed residue diet and intermediate in the pectin residue and brewers spent grain diets. Compared to the low fiber and basal diet the ATTD of N were lower in all fiber-rich diets.

Table 6.2.1 - Total tract digestibility of dry matter (DM), organic matter (OM), gross energy (GE), nitrogen (N) and fiber[1] in diets[2] fed to sows, in the three papers included in this thesis.

	Paper I[3]		Paper II				Paper III						
Item	LF	SBP	SBP	SH	PKE	MF	BD	SR	BSG	PH	PP	PR	SBP
DM, %	86	85	84	84	81	82	84	43	63	83	86	70	84
OM, %	89	88	88	87	84	85	87	47	65	85	87	71	87
GE, %	87	85	86	85	83	84	84	44	63	82	83	67	83
N, %	82	78	77	76	75	79	83	47	70	76	62	57	71
NSP, %	64	80	77	77	76	63							
cTF, %							66	14	41	76	87	64	88

[1] Non-starch polysaccharide (NSP) in paper I and II, calculated total fiber (cTF) in paper III.

[2] LF, low fiber (based on wheat and barley); SBP, sugar beet pulp; SH, soy hull; PKE, palm kernel expellers; MF, mixed fiber (SBP, oat hulls, wood fibers and yeast); BD, basal diet (based on barley) SR, seed residue; BSG, brewers spent grain; PH, pea hull; PP, potato pulp; PR, pectin residue.

[3] Average between early- and mid-gestation

6.2.1. Nitrogen digestibility

The ATTD of N was negatively affected by fiber inclusion, with the strongest correlation between ATTD and intake of insoluble NSP (paper II). However, in paper III the pea hull diet, with greatest insoluble NSP intake, did not statistically differ in the ATTD of N from the basal and sugar beet pulp diets. A similar high ATTD of N in pea hull compared to other fiber sources was also found by Jha and Leterme (2012), where the ATTD of N was 80.9 % when fed to growing pigs and with an apparent ileal digestibility of N of 74.4 % of the pea hull diet. This could indicate that the fiber matrix of pea hulls allows absorption of AA at the ileum and that the fiber matrix of pea hull with a high insoluble NSP to S-NSP ratio did not, increase the endogenous loss of N, and thereby increased the fecal N loss, resulting in lower ATTD of N (Jha and Leterme, 2012). On the other hand, sugar beet pulp had similar diet ATTD N in paper III as the basal diet, despite of a lower insoluble NSP to S-NSP ratio. In paper II the diet containing sugar beet pulp had the lowest insoluble NSP to S-NSP ratio followed by the MF, also containing sugar beet pulp. However, the mixed fiber had the greatest ATTD of N, followed by sugar beet pulp, both having ATTD of N in line with the greatest sugar beet pulp inclusion in paper I, and all being greater than in paper III. In paper III, the inclusion rate of sugar beet pulp was also greater, with the TF inclusion around twice as high as in papers I and II. The lowest ATTD of N was found in paper III in the seed residue diet followed by the pectin residue and potato diets with ATTD of N of 42 to 63 %, respectively, whereas potato pulp compared to all other diets used in this thesis has the lowest CP content, followed by pectin residue and seed residue. The combination of a fairly low CP content and ATTD of N has to be taken into account when formulating the diet. Perhaps more interesting was the palm kernel and brewers spent grain diets, that both have a high CP content, while having the lowest and intermediate ATTD of N, respectively, between the diets used in papers II and III.

6.2.2. Energy and OM digestibility

The energy digestibility was above 82 % in all fiber-rich diets in papers I and II and in the pea hull, potato pulp and sugar beet pulp diets in paper III. Here, pea hull, potato pulp and sugar beet pulp diets had similar ATTD of GE compared to the basal diet, while the low fiber diet in paper I had a ATTD of GE of 87%. The ATTD of GE decreased with increasing sugar beet pulp inclusion in early gestation in paper I. However, there was no difference between inclusion levels in mid gestation. This could indicate that feeding level influences the ATTD of GE, but looking at the feeding level in early (and mid) gestation in paper I, the ATTD of GE did not differ. This was in agreement with the findings of Casas and Stein (2017). Furthermore, no interaction between treatment and feeding strategy (not published) was found in paper I. Results from paper II and III do not indicate, that the average daily feed intake influenced the ATTD of energy. As an example, the average daily feed intake in the sugar beet pulp fed sows (paper III) with an intake of 4.6 kg/d was more than twice as high than in the basal fed sows, who got 1.9 kg/d, they did not differ in the

ATTD of GE. However, even if the sugar beet pulp fed sows are fed twice as high as the basal diet fed ones, it was still less feed than in peak lactation where a high feed intake has been shown to impair ATTD of what (Zhou et al., 2018a).
The ATTD of GE were greatest in the fiber-rich diets with high content of soluble fiber along with a low content of lignin; sugar beet pulp and soy hull in paper II and potato pulp, pea hull and sugar beet pulp in paper III. This was in agreement with Renteria-Flores et al. (2008), who found that the energy digestibility was higher when the diet was rich in soluble fiber compared to insoluble fibers. On the contrary, the mixed fiber diet in paper II has the same S-NSP as the soy hull diet and lower insoluble content, however soy hull has a greater ATTD of GE than the mixed fiber diet, due to a greater lignin content in the mixed fiber diet compared to the soy hull one. In the work done by Renteria-Flores et al. (2008) the diets compared were formulated to investigate the effect of the sum of hemicellulose, cellulose and lignin as insoluble fibers and not as different insoluble components. The same was the case in the work included in this thesis, and it shows that both the proportion between soluble and insoluble fiber as well as the lignin content influences the ATTD of GE.
Apparent total tract digestibility of GE was closely linked to the ATTD of OM ($r = 0.98$, $p < 0.001$; Table 4, paper II and $r = 0.99$, $p < 0.001$; not published). The ATTD of OM is a valuable tool when determining the energy value of the feed, as the ATTD of OM is the main factor in this determination (de Boever et al., 1986; Beecher et al., 2015). In paper II, the ATTD of OM was fairly close of the in vitro enzyme digestibility of OM (**EDOM**), with a difference between ATTD of OM and EDOM of ± 3.3 % point. In paper III, this was also greater in four of the seven diets; pectin residue and seed residue with greater EDOM than ATTD of OM (7.5 % units and 6.4 % units, respectively) and potato pulp and pea hull having lower EDOM than ATTD OM (-6.3 % units and -6.2 % units, respectively), while the basal, brewers spent grain and sugar beet pulp diets only differed 0.2, -0.3 and 1.9 % point, respectively. A study by Álvarez et al. (2020) found that the correlation between EDOM and ATTD of OM was high ($R^2 = 0.93$) in compound feed, which had a maximum neutral detergent fiber content of 36.1% DM. The largest bias was found with high neutral detergent fiber content, compared to CP, starch and fat, however, within the limits in EU regulation (Álvarez et al., 2020). In the current study, the diets used in paper I and II had a total content of lignin, cellulose and insoluble non-cellulosic polysaccharides (comparable to neutral detergent fiber) below the 36.1 % DM as did the basal, sugar beet pulp and potato pulp diets in paper III, while the others were above.

6.2.3. Fiber digestibility

The digestibility of fiber was not directly comparable between the three papers. In paper I and II we estimated the NSP digestibility, and in paper III it was calculated total fiber (**cTF**) digestibility. The difference being the inclusion of lignin in the cTF digestibility. It could be expected that through the inclusion of lignin, the cTF digestibility would be lower compared to the NSP digestibility if the same samples were analyzed (Rijnen et al., 2001). Comparing the different inclusion of sugar beet pulp, the ATTD of NSP increases with increasing sugar beet pulp inclusion ($P < 0.001$; Table 3, paper I), and the ATTD of NSP was slightly higher in paper II, with a ATTD of NSP of 77.5 % and with a TF inclusion of 196 $g \times kg^{-1}$ compared to 75.6 % in paper I with a TF inclusion of 185 $g \times kg^{-1}$ both was higher than the cTF ATTD of sugar beet pulp in paper III.

Compared to inclusion of the highly fermentable sugar beet pulp that increases fiber digestibility, inclusion of less fermentable fiber-rich co-product decreases the fiber digestibility, as shown by Mroz et al. (1986) where including oat hulls, high in insoluble fiber decreases the ATTD of neutral detergent fiber. Whether the digestibility increases or decreases will depend on the digestibility of the reference diet in relation to what is added/substituted and also what is compared. For instance, in paper II, the NSP digestibility was positively correlated to insoluble fiber, whereas in paper III, the ATTD of cTF decreased with increasing insoluble NSP content. This discrepancy was due to the type of diets compared; in paper II it was the mixed fiber diet that was the main driver for the positive correlation between the ATTD of NSP and insoluble NSP, whereas in paper III the correlation between insoluble NSP content and ATTD of cTF was not significantly different from zero.

6.3. Utilization of fiber-rich co-products in diets fed to sows

6.3.1. Energy utilization

Energy utilization can be divided into the metabolizable energy, including fecal, urinary and gas output, and the energy used for HP and retention.

Table 6.3.1 – Metabolizability, body weight (BW), heat production (HP) and heat production expressed pr. Kg metabolic body weight in sows fed fiber-rich diets[1], in the three papers.

	Paper I				Paper II				Paper III						
	d 0-30		d 30-60												
Item	LF	SBP	LF	SBP	SBP	SH	PKE	MF	BD	SR	BSG	PH	PP	PR	SBP
Metabolizability, %	82.4	81.1	82.9	80.9	79.8	82.2	79.2	80.5	79.5	42.6	57.3	77.1	77.3	63.0	76.8
BW, kg[2]	237	236	249	252	263	251	258	255	205	210	207	211	219	209	210
HP, MJ /d	28.9	26.9	29.9	25.2	27.5	26.9	26.5	28.8	23.3	23.4	23.4	24.8	22.7	23.4	23.2
HP, kJ/ $BW^{0.75}$ per day	478	447	477	399	422	427	412	452	430	425	429	447	399	425	421

[1] LF, low fiber (based on wheat and barley); SBP, sugar beet pulp; SH, soy hull; PKE, palm kernel expellers; MF, mixed fiber (SBP, oat hulls, wood fibers and yeast); BD, basal diet (based on barley) SR, seed residue; BSG, brewers spent grain; PH, pea hull; PP, potato pulp; PR, pectin residue.

[2] In paper I and II the BW was estimated from the initial BW and BW gain, assuming this was constant through the 30 or 60 days period.

The proportion between metabolizable energy and gross energy, termed metabolizability, varied between 79.2% to 82.9%, in all treatments in paper I and II together with basal, potato pulp, pea hull and sugar beet pulp diets in paper III Table 6.3.1. This shows that the energy in all these diets was well utilized by the sow. The metabolizability of brewers spent grain and pectin residue and particularly seed residue was somewhat lower. Noblet and Shi (1993) found a negative relationship between neutral detergent fiber and the metabolizability. This was not the case in the current study where the pea hull diet then would be expected to have a lower metabolizability. The reason for this was probably due to its low lignin content. Metabolizability of sugar beet pulp in paper II was similar to that of paper I, while it was slightly lower in paper III compared to papers I and II, but no statistical difference was seen between basal and sugar beet pulp diet in paper III. The basal diet was similar to sugar beet pulp in paper II and all treatments in paper I. Rijnen et al. (2001) found a decrease in metabolizability, as well as digestibility when exchanging tapioca with sugar beet pulp silage. This relationship between a decrease in metabolizability as well as digestibility was also found in the current study.

6.3.2. Heat production

The HP can be divided into maintenance HP, which includes energy used for absorption, digestive and cellular metabolic processes, thermal regulation and minimal physical activity (Ramonet et al., 2000b; Theil et al., 2020), and heat produced due to physical activity.

The majority of energy in all diets across the three papers was lost as heat, as also reported by others (Müller and Kirchgeßner, 1998; Theil et al., 2002). Energy lost as heat ranged in the current studies from 56% to 90% depending on diet.

Total heat production was lower in paper III compared to paper I and II, presumably due to the sows being lighter, as seen by the similar heat production when expressed per kg metabolic bodyweight, Table 6.3.1. In paper I the HP tended to be greater in the low fiber fed sows compared to the sugar beet pulp fed ones in mid gestation, as seen in the HP expressed as metabolic body weight as well, and thereby not due to a greater bodyweight. A decrease in HP expressed per metabolic bodyweight did decrease with increasing inclusion of sugar beet pulp which was also found by Rijnen et al. (2003).

in paper III the HP was divided into non-activity related HP and activity related HP, and was affected by fiber source. Sugar beet pulp and pea hull fed sows had the lowest activity related HP, while basal diet, seed residue, potato pulp and pectin residue fed sows showed the lowest non-activity related heat production. The activity related HP in paper III did not distinguish between types of activity, e.g. feeding (Brouns et al., 1994, 1997) and standing when eating or not eating like Ramonet et al. (2000b). Those studies showed that increasing the amount of sugar beet pulp, also increased the time spent feeding compared to a low fiber diet. In our study, the sugar beet pulp fed sows did stand numerically longer than all other sows except the seed residue sows. This could be due to increased time spent eating. Brouns et al. (1994) speculated that the increase in time eating was due to both an increase in the need for chewing and handling a bulkier diet with higher water binding capacity. Comparing the co-products used in paper III, pea hull had a low swelling capacity and potato pulp a high (Serena and Knudsen, 2007). The pea hull was served dry whereas potato pulp was served wet, but the time standing was similar between the two groups.

Therefore, the data from the current study cannot be used to distinguish between the time used for eating of the different diets as influenced by the fiber-rich co-product. Regarding satiety, no behavioral observations were done in the three papers included in this thesis and thereby stereotypic behavior as a satiety indicator can unfortunately not be included. Only total heat production was estimated in all three papers. In paper I, the total HP decreased numerically with increasing sugar beet pulp inclusion. This is in agreement with Jørgensen et al. (2010) and Rijnen et al. (2003), who found that increasing S-NSP content in the feed, compared to insoluble non-cellulosic polysaccharides, decreased the activity related HP. In paper III, it was sugar beet pulp and pea hull, rather than potato pulp, that had the lowest activity related HP, indicating that it was the intake of S-NSP rather than the content of the feed that causes the satiety. This correlates with the stretch receptors in the gut intestinal tract being activated when the gut is filled and thereby satiety is signaled (Paintal, 1954). Fermentation of fiber increases the fermentation heat, whereas the HP beyond digestion would be expected to decrease when SCFA is used in the *de novo* fat synthesis (Theil et al., 2020). Since the sows were fed close to maintenance in both paper II and III, the influence of fiber source on HP with simultaneous fat deposition could unfortunately not be investigated in the current experiments. However, in early gestation in paper I, fat gain did numerically increase with increasing inclusion of fiber, whilst the HP numerically did decrease. Whether this was solely due to reduced activity is not known, but it is plausible that it could be a combination of the shift between precursors for *de novo* fat synthesis as well as reduced activity.

6.3.3. Nitrogen utilization

The utilization of N was dependent on the energy balance throughout the day, protein intake, AA profile and ratio between protein and energy intake.

Table 6.3.2 - N intake, crude protein (**CP**) to gross energy (**GE**) and lysine to CP ratios in the diets used in the three papers

	Paper I[3]		Paper II				Paper III						
Item	LF	SBP	SBP	SH	PKE	MF	BD	SR	BSG	PH	PP	PR	SBP
N intake, g/d	45.6	50.4	43.0	45.0	55.1	47.2	37.3	38.6	60.3	25.1	49.6	26.0	30.6
CP to GE	7.38	7.71	7.06	6.53	6.86	6.39	7.30	5.85	9.46	5.51	7.33	5.49	6.50
Lysine to CP	0.047	0.042	0.046	0.047	0.039	0.046							

[1] Non-starch polysaccharide (NSP) in papers I and II, calculated total fiber (cTF) in paper III.

[2] LF, low fiber (based on wheat and barley); SBP, sugar beet pulp; SH, soy hull; PKE, palm kernel expellers; MF, mixed fiber (SBP, oat hulls, wood fibers and yeast); BD, basal diet (based on barley) SR, seed residue; BSG, brewers spent grain; PH, pea hull; PP, potato pulp; PR, pectin residue.

[3] Average between early- and mid-gestation

A high protein to energy ratio can limit the protein deposition due to protein being used as an energy source. This also limits the available energy due to deamination when catabolizing the excess amino acid to utilize the energy, which is energy demanding and increases N secretion in urine (Dourmad et al., 2008). The sow will, as discussed later, also mobilize fat, to use as energy and to retain protein.

Depending on the soluble fiber inclusion level and thereby fermentation, the nitrogen output can shift between fecal and urine. In paper I, fecal N output increases while the urine output decreases numerically with increasing sugar beet pulp inclusion. In this paper it was explained by 1) that the available metabolizable energy was greater, giving rise to a more optimal protein to energy ratio and/or 2) the diurnal fluctuation in energy uptake was lower (Serena et al., 2009) and thereby more energy was available throughout the day.

Due to the different CP intake when fed the different diets, it was not clear how the fiber-rich co-products influences the distribution between N lost in urine and in feces. However, except for brewers spent grain, pea hull and palm kernel expellers, fecal N output increases while urinary N output decreases when fiber-rich co-products was included in the diet, as found by others (Jarrett and Ashworth, 2018; Yang et al., 2021).

The ratio of protein to energy was comparable in the LF diet in paper I and basal and pea hull diets in paper III. However, the intake of the basal diet was lower causing a lower retention, whereas the intake from the pea hull diet was similar to that of low fiber in mid gestation, which gave rise to a similar retention. Except for brewers spent grain all other diets had a lower protein to energy ratio. The high protein to energy ratio in the brewers spent grain diet increased the urinary output, compared to the other co-products in paper III. This additional effect could be due to an imbalanced AA profile, which was not balanced depending on the co-product in this thesis. It was further not investigated whether the protein was damaged, eq. the Maillard reaction.

6.3.4. Retention of fat and protein

In relation to the thermodynamic theory, retention is the difference between intake and expenditure. However, in reality, it is not so simple. It is very dynamic and involves multiple feedback systems and ways for the body to compensate and adjust, also to individual responses (Casanova et al., 2019). Keeping it a bit simple, the expenditure of the early and mid-gestating sow covers maintenance, digestion, thermal regulation, physical activity, maternal gain and growth of conceptus (Dourmad et al., 2008). Some of these are rather stable during the day, while others will fluctuate. The size of retention is regulated by the difference between intake and expenditure whereas the retention of fat or protein is determined by many factors, including the composition of the diet and the genetics of the animal. High prolific sows will favor protein retention due to genetic selection, when fed at maintenance energy intake, sows will still retain protein, and mobilize fat if needed to cover the energy needed for that process (Pettigrew and Yang, 1997).

The requirement of protein will increase in an S-shaped curved throughout gestation, being low, with a SID lysine requirement increasing from just below 5 g/d to just below 8 g/d in early gestation reaching a plateau in mid gestation and then increase to above 12 g/d from d 80 to farrowing (Thomas et al., 2021). In early gestation this was below the Danish recommendation of 4.2 g SID lysine/kg equal to around 12 g SID lysine/d when fed 2.9 kg/d (Bruun, 2019; Tybirk et al., 2020). Assuming that the N requirement follows the same pattern, the N requirement in early gestation would increase from around 17 g N/d at estrus to around 28 g N/d at day 30 and around 28 g N/d from day 30 to 80 of gestation also assuming the same lysine to protein ratio. The N retention of 17 g N/d is perhaps a bit low but it was only the potato pulp in paper III with a N intake of 25.1 g N/d (not SID N intake), that has a negative N retention. However, none of the N retention in paper III was significantly different from zero. It should also be mentioned that the sows used in paper III were empty, not gestating.

Both the low fiber and sugar beet pulp diets in paper I were formulated to have similar SID lysine/kg diet. However, daily gain in the sugar beet pulp fed sows were greater than that of the low fiber fed sows, indicating an increased utilization of protein. This could be explained by an increase in the energy intake and potentially a lower diurnal fluctuation in energy uptake. This indicates that it was energy that was the limiting factor regarding protein retention in these sows. Regarding fat retention, the protein availability did seem to be too high to favor fat deposition, as seen in the study of Eskildsen et al. (2020a), a low protein intake, in late gestating outdoor sows, numerically increased fat deposition.

In neither paper II nor paper III retained energy as fat was different from zero, in any of the diets fed to sows. However, pea hull fed sows were superior to both seed residue and pectin residue fed sows due to a greater ME intake with the pea hull diet compared to the other diets in paper III. The most comparable diet to the pea hull diet, regarding ME and N intake was the highest sugar beet pulp inclusion in mid-gestation of paper I. The ME and the N intake of diet sugar beet pulp in mid-gestation are 27.3 MJ/d and 41.8 g/d, respectively, which can be compared to that of the pea hull diet in paper III, with a ME intake of 32.4 MJ/d and a N-intake of 49.6 g/d. The sugar beet pulp fed sows in paper I, retained 1.4 and 7.5 MJ/d in protein and fat energy retention, respectively, which was similar for protein but a bit lower for fat for the pea hull diet, where the sows retained 1.7 MJ/d and 5.7 MJ/d, respectively. This could indicate that sugar beet pulp was superior in terms of fat deposition, especially when taking into account that the ME intake of the sugar beet pulp sows were lower. However, the data for the body pool differed when using D_2O or energy balance, with a total retention of 8.9 MJ/d when using D_2O but only 2.1 MJ/d when using the energy balance. Although no comparable studies are available, it was assumed that the two methods for estimating fat deposition would give comparable results.

Between the treatments in paper II and brewers spent grain, potato pulp and sugar beet pulp in paper III there were no differences in fat deposition of the sows, as was the case regarding protein deposition, both around zero, in both papers due to the sows being fed close to maintenance. However, it is worth noticing that the energy retention found in the balances in papers I and II differed from the estimated change in body pools, especially in paper II where the palm kernel expellers stand out having the greatest retention looking at the balance, but the second lowest when looking at the body pools and BW gain. The BW gain and body pools were averaged over 30 days, while the balances were that exact day of difference between intake and output, the retention being the difference including uncertainties. Comparing the balances in papers I and II, the uncertainties will impact the results relatively more when retention was lower, as it was in paper II. In the palm kernel expellers, a poor pellet quality and thereby a potential feed loss, can potentially result in greater calculated retention, explaining the difference between the BW gain and body pools vs. balances.

6.3.5. Feed efficiency

Maximal feed efficiency can be obtained when the loss of nutrients from the body is minimized. This is done by feeding only what is required in the right proportions. For gestating sows this is done according to the stage of gestation, to ensure the optimal conceptus environment and towards achieving a certain BF level at farrowing, i.e. where skinny sows should restore their fat depots most efficiently, and while fat sows should be fed close to maintenance. To maximize the feed efficiency, both amount (the feeding strategy) and nutrient concentration of the feed should be optimized. According to Gaillard et al. (2021) optimizing the feeding strategy can reduce the lysine intake with 30% and excretion with 17%, when changing from a two phase (two levels and two diets) feeding strategy to precision feeding using day-to-day specific combinations of protein to energy ratios and feeding levels. In both papers I and II a multiple level feeding strategy (same diet) was used, in paper I, the multiple levels were further divided into three feeding strategies (low, medium and high feeding strategy), in accordance to the BF thickness of sows. Both the medium and low feeding strategy met the target goal for the BF level, whereas the skinny sows almost did, irrespective of dietary treatment. Only two out of 16 sows did not gain enough BF to move from the skinny to the medium feeding strategy at day 30, indicating that this period was a well-chosen period to feed the sow to gain fat, which is in agreement with Carrión-López et al. (2022).

With optimized feed according to the protein to energy ratio and AA to protein ratio, the urinary N loss and heat produced due to the deamination processes is expected to be minimized (Pedersen et al., 2018).

The energy cost above maintenance is a tool to plan the feeding of the sow in early and mid-gestation towards a BF (or fat pool) target. To calculate this the sows in paper I, early gestation fed the high feeding strategy, were chosen. The feed efficiency regarding restoring backfat was greatest with a TF content of 152 g, at an energy cost of 19 kg feed above maintenance / mm of backfat, while fat retention was just above 4.5 kg feed above maintenance / kg fat when the feed included 152, 185 or 217 g TF / kg, compared to 6 kg feed above maintenance when the feed only contained 119 g TF/ kg, Figure 6.3.2.

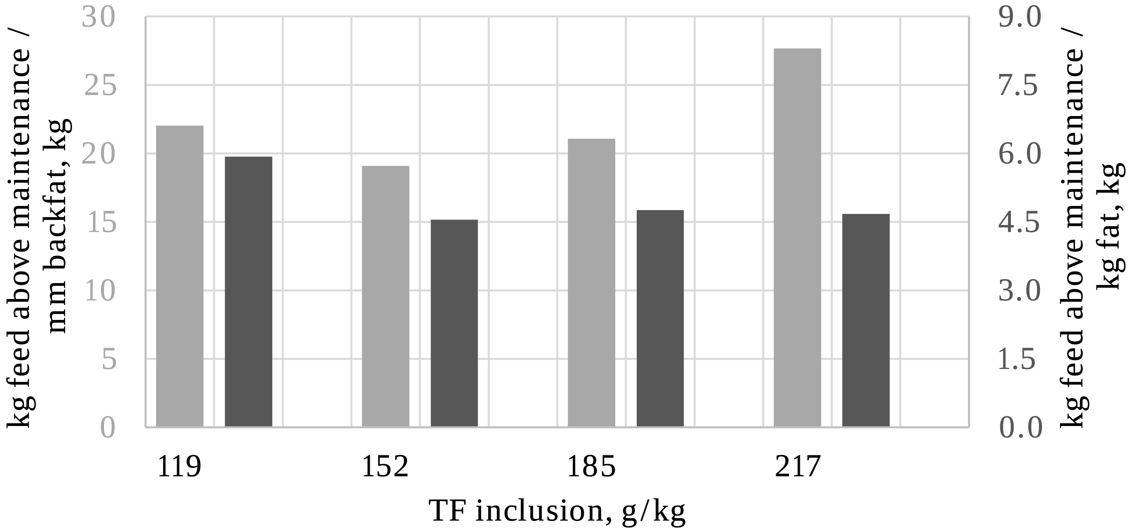

Figure 6.3.2 - The cost, in kg feed above maintenance, of retaining 1mm of backfat (BF) (light grey) or 1 kg fat (dark grey), depending on treatment, data from paper I, only including data from sows on the high feeding curve in early lactation.

Neither in mid-gestation in paper I nor in paper II did the feed efficiency differ between treatments. This indicates that there are no beneficial effects of including fiber in the diet on feed efficiency when the sow are fed close to maintenance, as the differences was hardly detectable. In contrast the tendency towards an increase in protein feed efficiency in early gestation with increasing sugar beet pulp inclusion emphasizes, that the sows have a high energy and N utilization, even with a high sugar beet pulp inclusion, when fed above maintenance. To turn this towards improvement of fat rather than protein retention, it is important to optimize the energy to protein ratio in the feed, by a more correct energy evaluation of fiber when fed to sows, especially those that need to gain fat.

SECTION 7. CONCLUSION

The central findings of this work are that all included fiber-rich co-products are suitable as ingredients in diets for empty, early and mid-gestating sows. Sugar beet pulp, pea hull, soy hull and the mixed fiber diet used, have a relatively high ATTD of energy (83 to 86 %) and all nutrients, making them well suited to partly substitute high value crops. For sugar beet pulp this was independent of inclusion level.
Palm kernel expellers, potato pulp and brewers spent grain were found to compromise the N utilization. The diets with seed and pectin residue had fairly low ATTD of both energy (44 and 76%, respectively) and nutrients, making them suited as gut fill, however with a low nutritional value.
The differences in ATTD were according to fiber composition, and especially the degree of lignification negatively affected ATTD of both energy and nutrients.

The energy from these co-products were, when absorbed in the intestine, well utilized. Unfortunately, the sows still favored protein deposition since fat deposition only increased numerically with increasing sugar beet pulp inclusion. The low feeding level applied in papers II and III limited the retention of especially fat, and thereby no effect of different fiber sources, on re-storing of fat including backfat, were found in this study.

We did not find differences between fiber sources on the total heat production. A distinction between activity and non-activity related heat production was not estimated in papers I and II. In paper III, sows fed seed residues had the greatest activity related heat production, this could indicate that sows felt hungry, on the contrary, the sows receiving sugar beet pulp and pea hull were least active, likely due to them having a greater feeling of satiety.

SECTION 8. FUTURE PERSPECTIVES

The future perspectives related to the use of co-products as feed ingredients in diets to early and mid-gestating sows should be focusing in-depth on N utilization with the aim to optimize it and to avoid excess N excretion. Optimizing this may be a key feature in achieving a circular food system. Focus here could be in different aspects, e.g.:

- How can lower diurnal energy fluctuation affect N-utilization and whether the utilization at the same time is affected by amino acids origination from protein sources or crystalline sources.
- More in-depth knowledge about diurnal fluctuations in the energy balance and how this affects the use of essential AA as an energy source.
- Provide a broader insight in the degree of heat-damaged AA in different co-products.

Another topic only briefly touched upon in this thesis is the methane production. In future research this should be in focus, due to it having a substantial environmental impact. A methane focus should perhaps be accompanied with the scope of improving the N-utilization, which may be of greatest interest.

When conducting further research on retention of fat and protein, caution should be taken in aiming for a higher retention to minimize effects of uncertainties when using balances to estimate the retention.
If focus is on distinguishing between fat and protein retention it would be of great general interest to validate the Rozeboom et al. (1994) equations derived from gilts in 1994 when using the deuterium technique. This would include going into depth on the precision of the detection level of and between changes in the different body pools.

Another focus could also be, to look more in-depth at the relationship between ATTD of OM and EDOM, especially focusing on potential interaction between ingredients. Álvarez et al. (2020) evaluated and reported additive properties of the chemical components of compound feed on digestibility of OM and EDOM. However, they did not focus on fiber-rich feedstuff nor ingredients.

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APPENDIX

Estimating urinary nitrogen excretion based on 6h or 24h collections

This experiment was carried out to test the hypothesis that the hourly urinary nitrogen (N) excretion is constant meaning that 6 hours collection can be used to estimate 24 h urinary N excretion.

Materials and method

Eighteen gestating multiparous (mean bodyweight 268 kg ± 50) crossbreed sows (DanBred Landrace × DanBred Yorkshire) had in the morning (0800 – 1000 h) a urinary balloon catheter (Teleflex Medical, Kamunting, Malaysia) size 20, inserted. A clamp was placed just where the catheter was out of the urinary tract, to prevent the catheter from sliding back and forth in the urinary tract and thereby cause urinary infection. Two sows, however, were omitted; one because an unknown amount of urine was lost, and the other sow because the urine had an odd color.

The bladder was emptied just before the start of the collection period, a stopper was placed around the catheter and the time noted. Every second hour, the catheter was emptied with a hose into a 10L container and kept cool between collections. After approximately 6 hours the catheter was emptied first with the hose and then a cup, to ensure that all urine produced up to that time point was collected, while the sow kept its chosen position. Weight of the bucket and a subsample were kept at -20 degrees awaiting further analysis. For the following 18 hours, urine was collected every second to fourth hour following the same procedure as during the first 6 hours and at the end of the 18 hours collection period the urine was weighted and a subsample collected as described for the 6 hours collection.

Urine nitrogen was analyzed using the Kjeldahl method (method 984.13; AOAC Int., 2000) on a KjelTecTM 2400 (Foss, Hillerød, Denmark).

Results are presented as 24 hours nitrogen excretion by extrapolating from 6 to 24 hours and total (sum of 6 hours and 18 hours collections). Calculations and correcting that the collection time was not always exactly 6 and 18 hours, were done according to the following, with nitrogen as an example:

Extrapolation from 6h collection: $N\ [g/d] = N_{0-6h}[g/kg] \times \frac{Urine_{0-6h}\ [kg]}{Collection\ period[h] \times 24}$

Total collection:

$$N\,[g/d] = N_{0-6h}[g/kg] \times \frac{Urine_{0-6h}\,[kg]}{Collection\,period[h] \times 6} + N_{6-24h}[g/kg] \times \frac{Urine_{6-24h}\,[kg]}{Collection\,period[h] \times 18}$$

The data were analyzed using the MIXED or GLM (only the figure) procedures in SAS (version 9.4, SAS Institute Inc., Cary, NC, USA, 2012), with extrapolation and total as the fixed effects and sow as repeated variable. The results are presented as means ± standard error of means (SEM), where the highest SEM is shown. A probability value between $0.05 < P \leq 0.10$ was considered a tendency, while significant when $P \leq 0.05$.

Results

The amount of urine produced tended to differ between methods; mean 777 g/h (range 650 to 2197 g/h) when extrapolating and mean 624 g/h (range 54 to 1589 g/h) for total collection ($P = 0.07$; Table A.1.1). No difference between extrapolating or total collection was found in either N concentration (P=0.46) or excretion per day ($P = 0.41$; Figure A.1.1). There was a significant difference in total amount urine collected and nitrogen concentration between sows (P < 0.01; data not shown), nut with no difference in nitrogen excretion per day (P = 0.12; data not shown).

Table A.1.1 - Urine collected and nitrogen concentration and excretion in gestating sows extrapolated from 6h collection and for a total period of 24 h

Item	Extrapolating	Total	SEM	*P*-value
n	16	16		
Collection period, min[1]	365	1447		
Amount collected, g/h	777	624	56	0.07
Nitrogen, g/100g	0.37	0.29	0.071	0.46
Nitrogen, g/d	23.0	21.6	1.154	0.41

[1] Not corrected for time

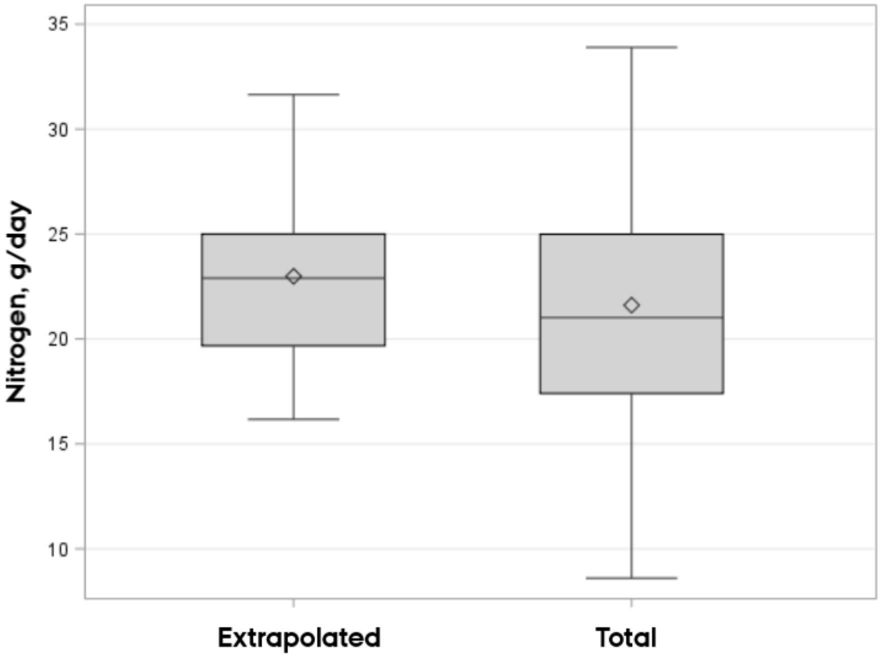

Figure A.1.1. Nitrogen excretion g N per day when extrapolated from 6h collection and for a total period of 24h.

Conclusion

It is possible to use 6h collection of urine to estimate 24h N excretion in gestating sows.

Fiber-rich co-products, such as sugar beet pulp, soy- and pea hulls are of increasing interest as feed ingredients in sow feed. Co-products not directly suitable for human consumption can re-enter the feed chain as human food through animals. These co-products are a diverse group of fiber-rich ingredients, and the knowledge of the energy value is limited, but important when feed is optimized, due to both health of the animal and environmental effect of output of nutrients.

Determination of the digestibility and thereafter utilization of both energy and nutrients from different fiber-rich co-products in diets fed to dry sows, is what this thesis is about.